Predicting ecological impacts of climate change and species introductions on a temperate chalk stream in Southern Britain - a dynamic food web model approach.

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Abstract

To predict the impact of future disturbances such as climate change and introductions of non-native species on ecosystems, it is important to understand how disturbances may affect community composition. This is inherently difficult since species may be expected to respond differently to disturbances such as elevated temperatures or the introduction of a new species. Furthermore, since the species in an ecosystem are interlinked by energy, nutrient and information transfers, disturbances may be amplified or absorbed, depending on the nature of the disturbance and the resilience of the ecosystem. Some species have a disproportionate effect on ecosystem function and are often referred to as keystone species. By definition the loss of a keystone species causes a catastrophic change in community composition. Therefore, the identification of keystone species could help to target conservation efforts more efficiently. A dynamical food web model, representative for a chalk stream (the River Frome, Dorset) was developed and manipulated. Changes in community composition and biodiversity were assessed. For the identification of keystone species each species node was removed in turn. Although impacts were found, particularly after the removal of important prey nodes and top predators, no catastrophic shift was observed and, consequently, no keystone species were identified. Impacts of species introductions were assessed by adding representative model species to the food web. The largest impact was observed after the addition of a small competitor at intermediate trophic level. The addition of a top predator had moderate impact, whereas no negative impact was found after the addition of a larger bodied species at intermediate trophic level. Possible impacts of climate change, specifically elevated temperatures, were assessed by increasing the metabolic rates of the species nodes. No impacts were found, when energy inputs were raised accordingly, but severe impacts, were observed when energy inputs were restricted. In general, the ecosystem was considered fairly resilient to most of the tested disturbances, possibly owing to the high natural variability of the community. The findings of current study suggest that rather than focusing conservation efforts on single species, the focus should be on 'keystone structures' that maintain high ecosystem resilience.

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Chapter 1

Introduction

The diversity of life, or biodiversity, is a defining feature of natural ecosystems. Organisms are connected through a complex network of biological interactions, energy fluxes and the associated physical factors that comprise the environment. Together these govern ecosystem processes (Willis, 1997). Ecosystems differ in size, structure, and community composition and perform essential functions such as decomposition and waste materials processing, nutrient-recycling, and secondary production (e.g. Cummins, 1974; Daily, 1997). Consequently, ecosystems provide important goods and services to mankind, from the provisioning of basic needs such as food and water up to cultural services such as recreational, intellectual and spiritual inspiration (Costanza et al., 1997).

Since the beginning of agriculture 11,000 years ago, "humankind has increasingly appropriated the biological resources and natural productivity of lands and seas to support the expansion of civilisations and technologies" (Groombridge and Jenkins, 2002). However, as a result of the increase in human population, the pressures on natural ecosystems are also increasing with direct effects on the ability of ecosystems to produce goods and support their associated services (Baron et al., 2002; Nilsson and Renofalt, 2008). Historically, pollution and land use change were the primary factors impacting ecosystems at local and regional scales. With the recognition of climate change, impacts are expected to be observed at a global scale with

unforeseeable consequences on biological communities (Schiedek et al., 2007; Grimm et al., 2008). A healthy ecosystem is resilient to external disturbances without losing its essential functions, or is able to recover relatively rapidly after being impacted (De Leo and Levin, 1997). However, measures of ecosystem resilience to specific disturbances are difficult to characterise despite their crucial importance to help underpin adaptive conservation policies and management measures. Consequently, it is becoming increasingly important to predict future global impacts on ecosystem function (Lal, 2007; Grimm et al., 2008; Morais, 2008).

Ecosystem function is dependent on food web structure, such as the degree of complexity or food chain length (Montoya et al., 2003; Thebault and Loreau, 2003). The choice of the food web boundaries can influence food web structure, but is often not easy to define, because ecosystems often have overlapping communities and energy exchange (Knight et al., 2005; Power, 2006). Locality, time, distinct abiotic and biotic factors, community structure and function have been used to define ecosystem boundaries (Post et al., 2007). For instance, three broad types of ecosystems (terrestrial, marine and freshwater) are defined. Within each of these categories, ecosystems can be discriminated on a climatic basis, such as arctic, tropical, and temperate. However, segregation within a single climatic zone can also be divided in sub-ecosystems such as forest, grassland, pelagic, benthic, lentic, and lotic. All these boundaries are structural, whereas functional boundaries can be described on the basis of material and energy flow, species interactions and movement of organisms. For example, steep gradients in the exchange of nutrients and energy at a certain locality indicate a functional boundary. Often these functional boundaries are mediated by structural boundaries (Post et al., 2007). In particular, lakes or islands are well-bounded systems, in both functional and structural aspects. In comparison, streams pose less bounded systems especially on larger temporal scales. This is mainly due to hydrological characteristics that can cause changes in the watercourse (structural boundary) and energy exchange with marine or terrestrial systems that can be highly variable because of allochthonous input or nutrient transfer through anadromous species (functional boundary). The definition of ecosystem boundaries

can therefore have profound consequences to the outcome of experimental or theoretical approaches that investigate ecosystem processes (O'Neill et al. 1986).

Freshwater ecosystems are excellent candidates for studying human induced impact on ecosystem function for a number of reasons. Firstly, freshwater systems provide important services such as drinking water, fisheries, transport routes and recreational activities (Costanza et al., 1997; De Leo and Levin, 1997; Holmlund and Hammer, 1999; Wilson and Carpenter, 1999; Nilsson and Renofalt, 2008). Secondly, they are experiencing increasing pressure, which is rapid and dramatic at high altitudes and latitudes (Sala et al., 2000; Malmqvist and Rundle, 2002). Particular disturbances of riverine ecosystems include chemical and thermal pollution, discharge regulation and water abstraction. For instance, changes in the natural discharge regime have been shown to have a negative impact on aquatic species diversity (Poff and Ward, 1989; Mann and Bass, 1997; Sheldon and Walker, 1997; Dewson et al., 2007; Morais, 2008). Another increasing source of disturbance is the introduction of non-native species, which may have major consequences for community composition (Vander Zanden et al., 1999; Koel et al., 2005; Baxter et al., 2004; Gozlan et al., 2010b). Thirdly, freshwater ecosystems have relatively manageable food webs in terms of both, data availability (e.g. well quantified diet compositions) and relatively well defined ecosystem boundaries.

For the above reasons (i.e. socio-economic importance, level of disturbance, well established energy transfers, and manageable food web size), the development of a dynamic food web model for a lotic freshwater system presents a realistic opportunity to generate effective and meaningful predictions about the impact of climate change and the introduction of non-native species on biological communities and ecosystem function. Disturbances expected to affect freshwater ecosystems in the future are: *i*) additional structural changes (e.g. river regulation, hydropower stations, land-use change; Sheldon and Walker, 1997; Pilcher et al., 2004), *ii*) changes in temperature and discharge (FSBI, 2007), and *iii)* biological invasions (Gherardi et al., 2008; White et al., 2008; Gozlan et al., 2010b).

Structural changes alter aquatic habitats and can lead to species displacement due to altered community composition (Morais, 2008). Human-induced disturbance on ecosystems can be studied either by analysis of historic data, through *in situ* and *ex situ* manipulation experiments, and/or computer simulations (Power, 1990; Hastings and Powell, 1991; Green and Sadedin, 2005; Power, 2006). Although historic long term datasets are often sparse and incomplete, these data can still provide valuable information on ecosystem behaviour and intrinsic variation. They can deliver the foundation for building reliable ecosystem models, which may be used to understand underlying mechanisms and predict future conditions (Holmes, 2006). Manipulation experiments (i.e. large scale field experiments or small scale laboratory experiments) are also important for hypothesis testing and model validation (Rykiel, 1996). Although large scale field experiments are ideal, they are expensive and rare because they may cause major collateral disturbances to an ecosystem (Lampert and Sommer, 1999) and it may be difficult to control environmental factors (e.g. temperature) in a systematic way. Contrary, laboratory experiments offer the opportunity to manipulate conditions precisely, but results have to be scaled up to real ecosystems. This approach may be limited in its capacity to reproduce ecosystem function and therefore in its overall relevance to test the impact of disturbances on ecosystems (Carpenter, 1996b). Comparison of already disturbed ecosystems to similar pristine ones can be an alternative solution to large scale field experiments.

A further and extremely promising approach is ecosystem modelling, which has become increasingly prominent in recent years (Green and Sadedin, 2005). As the available computing power limits model complexity, models should be kept as simple as possible to prevent the creation of one complex system to understand another complex system (Voinov, 2002). According to Deming "All models are wrong, some models are useful" (McCoy, 1994). The modelling process itself is as valuable for the understanding of a system as the final outcome. For example, in consideration of questions such as: Which parameters are important and which are superfluous for the generation of prediction? What rules or algorithms govern the system? Is the choice of the model and parameters objective or was it made subjectively in anticipa-

tion of an expected answer? Although theoretical approaches are useful for finding general rules for ecosystem behaviour, a hands on approach is needed to put conservation plans into action (IPCC, 2007). More specific models for particular types of ecosystems need to be developed and ecosystem structure, dynamics and function have to be linked to fulfil this demand (Martinez et al., 2006; Thebault and Loreau, 2006; Thebault et al., 2007; Jordan et al., 2008). Food web simulation experiments mimic the real ecosystem in a simplified way that allows easy and quick tests of different conditions with a high number of replicates. Simulations are cost effective and valuable tools for isolation of trends, which can then be verified experimentally (Green and Sadedin, 2005). Particularly in the context of environmental change, food web models offer a more realistic approach to identification of the impacts of stressors compared with traditional population studies (Perkins et al., 2010).

Climate change

Global average temperatures have risen by nearly 0.8°C since the late 19th century, with an increase of 0.2°C per decade in the last 25 years as a result of climate warming (Jenkins et al., 2008) and are predicted to increase a further 1.4–5.8°C in the next century (IPCC, 2007). Mean annual temperatures in Southern England have risen by 1.4–1.8°C between 1961 and 2006 ($\approx$ 0.3°C per decade; Jenkins et al., 2008). This has triggered species range shifts northwards and to higher altitudes in aquatic taxa (Hickling et al., 2006). Temperature also influences the reproductive success of aquatic organisms, since hatching success, and egg and larval development time is strongly temperature dependent (Guma'a, 1978; Pauly and Pullin, 1988; Planque and Fredou, 1999). Furthermore, the distribution of parasites and pathogens is affected directly and indirectly (through host range shifts) by global warming and transmission rates and virulence are expected to increase (Marcogliese, 2008). For England and Wales, although the annual mean precipitation has not changed significantly since the records began in 1766, in the last 45 years, heavy precipitation events in winter became more frequent, whereas in summer they have decreased (Jenkins et al., 2008). This trend is predicted to continue (IPCC, 2007). Changes

in magnitude and timing of precipitation events have direct affects on the discharge regimes of lotic freshwater systems. Shifts in natural flow regimes have been shown to affect biodiversity and community composition (Poff and Ward, 1989; Mann and Bass, 1997; Sheldon and Walker, 1997; Baron et al., 2002; Dewson et al., 2007). In a comparative study, macroinvertebrate abundance and diversity showed both increases and decreases as a response to elevated and reduced discharge, whereas fish abundance and diversity decreased in both cases (Poff and Zimmerman, 2010).

Invasive species

Invasive species have had a demonstrable impact on community structure in invaded ecosystems (Baxter et al., 2004; Koel et al., 2005). Indeed, biological invasions and the induced changes in the abundance of species have been shown to elicit stronger direct and indirect effects on food webs in freshwater systems than in terrestrial or marine systems, possibly because freshwater systems are relatively more closed systems regarding energy transfer boundaries than terrestrial or marine systems (Vander Zanden et al., 1999; Shurin et al., 2002; Hall et al., 2007). The introduction of non-native species that might subsequently become invasive is facilitated *via* anthropogenic pathways such as aquaculture and fish stocking (e.g. Copp et al., 2010a,b; Gozlan et al., 2010b). There is some evidence that changing climatic conditions might also benefit non-native species that have not previously been able to establish a sustainable population due to unfavourable temperatures (Gherardi et al., 2008; White et al., 2008). The prediction of combined impacts of climate change and non-native species introductions on aquatic community structure is difficult, since ecosystems are complex self-organising systems (Kay, 2000). Simultaneous changes in several state variables can cause system behaviour that cannot be deducted from responses to changes of single state variables (*cf.* Chapter 2). Temperature, discharge and carbon dioxide (CO_2) concentrations act on food web structure and dynamics differently, e.g. metabolic rates, mortality and palatability (Peters, 1983; Mion et al., 1998; Rier et al., 2002; Tuchman et al., 2002; Wright et al., 2004; Dewson et al., 2007; Power et al., 2008).

Keystone species

Within a food web, species exhibit interactions of varying importance. Some exert a disproportionally large effect on food web structure (Paine, 1969a). These "keystone" species stabilise the ecosystem, and the effect of their removal cascades through the food web, changing species abundance of directly connected species (through feeding links) and indirectly on to other levels of the food web (Power and Tilman, 1996; Schmitz, 2006; Woodward et al., 2008). The ecosystem shifts into a new state with unknown consequences on ecosystem function and services. The identification of keystone species also constitutes a robust approach to conservation by identifying conservation priorities, and adds to the mechanistic understanding of the ecological processes. Potential keystone species that have been identified by modelling approaches can then be verified in small scale exclusion experiments.

Aims and Objectives

The aim of the present study is to identify impacts of environmental change on community structure and biodiversity using a food web modelling approach.

Objectives are:

1. Develop a quantitative dynamical food web model for a temperate chalk stream.
2. Assess impacts of single species loss on food web structure.
3. Assess impacts of single species introduction on food web structure.
4. Assess impacts of increased temperature on food web structure.

Structure of the thesis

The thesis contains seven chapters plus references and appendices. Chapter 2 is a literature review on the characterisation of food webs, and introducing food web

concepts and mechanisms. Within Chapter 2, there is discussion of how the understanding of food web dynamics can add to the understanding of ecosystem processes and, ultimately, ecosystem services. Chapter 3 describes the development of the dynamic food web model that is used in the three subsequent chapters to test the impact of the different disturbances. Chapter 3 also includes the description of the study site from where the empirical data were collated and the description of the modelling software. Assumptions behind the development of the "Baseline Model" are discussed in regard to advantages and limitations. In Chapter 4, the impact of single species removal is investigated to identify possible keystone species in the ecosystem. Methods to assess change in community structure and ecosystem function are introduced and applied, and implications for the stability of this kind of ecosystem are discussed. In Chapter 5, model species with different characteristics are introduced into the food web model and the consequences on food web structure and ecosystem function are assessed with the same methods used in the previous chapter. Chapter 6 investigates possible impacts of climate change, concentrating on two aspects: *i*) temperature rise, which has direct consequences on metabolic rates; and *ii*) energy limitation as a consequence of changes in leaf litter chemistry, triggered by rising carbon dioxide concentration in the atmosphere. For the characterisation of impacts, the same methods as in the preceding chapters are used. The general conclusion (Chapter 7) discusses possible combined impacts of the tested disturbances and consequences on ecosystem function and services. Implications for conservation plans and future research are explored.

Chapter 2

Review of food web characterisation.

2.1 Introduction

The study of aquatic food webs has expanded greatly in recent decades. A Google Scholar search for the term "food webs" (in "document title") revealed that the amount of published studies have doubled every decade since 1980. Novel, theoretical and empirical approaches have been developed to identify the underlying mechanisms of the complex trophic interactions of organisms (e.g. food web topology: Borer et al., 2002; Dunne et al., 2002a; Montoya and Sole, 2002; dynamic approaches: De Ruiter et al., 1996; Sole and Valls, 1992; and stable isotope analysis: Hecky and Hesslein, 1995; Vander Zanden and Rasmussen, 1999; Vander Zanden et al., 1999). Food webs are graphical representations of nutrient or energy flows among species or functional groups of a community, and consist of primary production, consumption and decomposition with variable complexity (Pimm, 1982). The structure of food webs determines ecosystem function, and Wilbur (1997) suggests that "food webs are a central, if not the central idea in ecology".

The study of food webs goes back to the start of the 20th century, triggered by the need to assess fish stocks (Belgrano et al., 2005). Later, the interconnection of

community stability and food web complexity was investigated (MacArthur, 1955), followed by studies that assessed the importance of single species for community stability (Paine, 1966). Recently, advances in network analysis have given rise to new modelling approaches in the study of ecological community stability (Berlow et al., 2004; Dunne et al., 2004; Ulanowicz et al., 2006; Duffy et al., 2007; Jorgensen, 2007; Montoya and Yvon-Durocher, 2007; Uchida et al., 2007; Berlow et al., 2008; Rall et al., 2008).

Healthy ecosystems, in particular aquatic systems, provide mankind with important goods, such as food and water and with services, such as nutrient recycling (De Leo and Levin, 1997; Holmlund and Hammer, 1999; Nilsson and Renofalt, 2008). However, the availability of these goods and services can change when an ecosystem is permanently disturbed (De Leo and Levin, 1997; Power, 2006). Under natural conditions, ecosystems have evolved towards an equilibrium or a set of dynamic equilibria where, over a period of time, species diversity and biomass is maintained (Holling, 1973; Vandermeer and Yodzis, 1999; O' Neill, 2001). Serious disturbances can shift the ecosystem state to a markedly different equilibrium (Vandermeer et al., 2004), with consequences on ecosystem function. The present chapter explores the mechanisms that influence food web structure and dynamics and how the understanding of these mechanisms can benefit the understanding of ecosystem processes and ecosystem services.

2.2 Classification of organisms

In aquatic ecosystems, the flux of energy via predator-prey interaction is generally directed from small-sized, short-lived, abundant organisms with high nutrient turnover rates to larger, long-lived, rare species that fix nutrients for longer time periods, thus making this energy unavailable (Nakazawa et al., 2007; Ings et al., 2009). Food webs can be described not only by species interactions but also by interactions between groups of species, such as guilds (Root, 1967; Davic, 2003) or functional

groups (Cummins, 1974) and the way of grouping species depends on the question asked.

Although the terms are sometimes used synonymously, the members of a guild share similar resources that are exploited in a similar way, whereas members of a functional group perform similar ecosystem processes through resource exploitation (Blondel, 2003). The concept of the functional group was developed to investigate the theory that distinct communities are constructed from the same fundamental units (Jaksic, 1981; Blondel, 2003). By exploiting the same resources, members of a guild compete with each other, consequently intra-guild competition is higher than inter-guild competition (Pianka, 1980; Jaksic and Medel, 1990). Guild members are often, but not necessarily, closely related (Jaksic, 1981) and they form a structural component of an ecosystem, comparable to a building block. If a member of a guild is removed, then competition is reduced and the abundance of other guild members is expected to change, as the remaining guild members can now exploit more of the resource.

Since functional groups are defined as performing a similar ecosystem process (e.g. water uptake, storage of resources, pollination), they are ecologically equivalent and add redundancy to the ecosystem (Cummins, 1974; Körner, 1993). The term redundancy is used to describe species that fulfil the same function (ecological redundancy, Walker, 1992; Lawton, 1993). The negative connotation of the term suggests that some species are superfluous and their loss would not affect ecosystem function, but redundancy is regarded as increasing ecosystem integrity and resilience and is therefore valuable (Naeem, 1998). Removal of a member of the functional group will have no effect, when redundancy is high. However, low redundancy within the functional group can lead to altered ecosystem response (Blondel, 2003). Functional groups are often across-taxon-assemblages, with the members showing similarities in a functional context. During ontogeny, species can belong to different guilds and functional groups (Werner and Gilliam, 1984). This is particularly true for lotic systems (Cummins, 1974). Gitay et al. (1996) argue that the concept of redundancy should be abandoned because of its uncertainties and impracticalities for conservation. The term is easily misunderstood and the difficulties arising from defining a

redundant species are numerous. Despite those objections to the terminology, ecological redundancy can be viewed as insurance to respond to environmental change, while sustaining dynamic ecosystem regimes (Elmqvist et al., 2003).

Size is an appealing measure by which organisms can be grouped. It is easily measured and therefore a convenient parameter for biological assessment. In aquatic food webs, most predators are restricted to prey that are smaller than their gape size, so body size and the organism's possible trophic relationships are correlated. Aquatic organisms that belong to different size categories during their life-cycle change and expand their diet during ontogeny (Cummins, 1974). It has been suggested that body size is often the stronger determinant for trophic position than taxonomic classification (Woodward et al., 2005a; Petchey et al., 2008) and high diet overlap among similar-sized organisms has been found (Woodward and Hildrew, 2002). Feeding links between species cannot only change in strength, but also in direction. For example, large instars of caddisfly larvae prey upon alderfly larvae, but alderfly larvae prey upon small instars of caddisfly larvae (Woodward et al., 2005b). Predatory fish show clear ontogenetic shifts in their diet. Pelagic rotifers and phytoplankton are the main food resource for newly hatched fish, but, as the fish develops, micro-crustaceans and chironomid larvae become more important (Nunn et al., 2007). Adult fish prey mainly on macroinvertebrates or insects (Mann and Orr, 1969) and some become piscivorous, such as northern pike (*Esox lucius*) (Mann, 1980b). Body size also seems to be linked to various other characteristics, such as home range, population density, and metabolic rate. All of these examples highlight the importance of including body size in models of species interactions (Peters, 1983; Jonsson and Ebenman, 1998; Loeuille and Loreau, 2006).

Species mobility is another important factor, because mobile species create linkages among food webs or subsets of food webs (Winemiller and Jepsen, 1998). The habitat and home-range of an organism determine the interactions this organism can have within the stream food web, with the intensity of the interaction determined by the frequency and duration of encounters (Dodds, 2002). Lotic ecosystems are patchy, being composed of different habitats such as pools, runs and riffles. Redistribution

of nutrients across habitats and ecosystems may have important implications for food web dynamics (Polis et al., 1996; Polis and Hurd, 1996a,b). For example, sessile organisms, such as net-spinning caddisflies filter by-passing food out of the water column in contrast to Atlantic salmon (*Salmo salar*), which is a highly mobile species that migrates between streams and the sea. Migratory behaviour also adds temporal variations to food web dynamics. An entire body of research exists about the importance of nutrient input into rivers and streams of North America by Pacific salmon (*Oncorhynchus* spp.; see Cederholm et al., 1999). Once a year, adult Pacific salmon migrate back to their birthplace to spawn and die afterwards. The carcasses pose an important, marine-derived nutrient input into the freshwater and terrestrial ecosystems. In general, a nested hierarchy emerges (Woodward et al., 2005a) where patches that are inhabited by species with small home ranges are connected by more mobile species.

2.3 Mechanisms and concepts of food webs

2.3.1 Ecosystems as self-organising systems

Ecosystems are self-organising complex systems (Kay, 2000; Sole et al., 2002) in which organisms (i.e. parts) are interconnected through energy and material flow, governed by positive and negative feedback loops. Emergent behaviour of self-organising systems (a behaviour that cannot be deducted from the properties of the parts) is a common phenomenon and at any one moment in time these systems are defined by a set of variables, such as species diversity or productivity (i.e. state). The sum of all available combinations of variables (i.e. the sum of states) forms the self-organising system's 'phase-space' or 'state-space'. The ensemble of states, which a dynamical system approaches from any other location in the phase-space is called an attractor. The area of phase-space that leads to an attractor is called a domain (or basin) of attraction. An attractor can be a single point, a periodic orbit, a limit cycle, or a chaotic trajectory (strange attractor) (Sole and Bascompte, 2006).

Feedback systems, such as ecosystems, organise around attractors. As a consequence, the system's environmental situation can change, but as long as the system state is still within the domain of attraction, the system does not perform a shift (Kay, 2000). The positive feedback loops stabilise the system so that it maintains its current state. When the system is moved too far from its current attractor into a different domain of attraction, the changes that occur tend to be rapid and catastrophic as the system shifts. When a shift will occur and how the new state will be characterised is hard to predict, because there are often several possible attractors. A classic example of a system with at least two attractors is the natural process of eutrophication, which is particularly evident in shallow lakes (e.g. Blindow et al., 1993; Scheffer, 1990; Scheffer et al., 1993; Carpenter and Cottingham, 1997). State 1 is oligotrophy, which is defined by low productivity and transparent (clear) water, often with submerged vegetation. State 2 is mesotrophy, an intermediate state, which is defined by moderate productivity and water turbidity. State 3 is eutrophy, which is defined by elevated productivity, high phytoplankton density and increasingly turbid water with little or no submerged vegetation. High nutrient input (e.g. as a result of fertiliser use in agriculture) will shift the system from state 1 into state 3. To return to state 1, nutrient levels have to be reduced substantially. Other than reducing the nutrient levels, a reduction of predatory fish that feed on phytoplankton grazers, such as *Daphnia*, can shift the system back to state 1. Zooplanktivore fish control phytoplankton grazers, which control phytoplankton. Phytoplankton reduces sunlight availability and therefore inhibits growth of submerged vegetation. A decrease of zooplanktivore fish has a positive effect on the phytoplankton grazer population and an (indirect) negative effect on phytoplankton. With decreasing phytoplankton biomass, turbidity decreases and the conditions for plant growth improve. A further increase of water clarity induced by vegetation creates the right environment for plant growth (a positive feedback loop), therefore the system stabilises itself again. State 3 is also stabilised by a positive feedback loop. An increase in phytoplankton biomass increases turbidity, so phytoplankton can out-compete submerged vegetation. A similar process of eutrophication happens in flood plain hydrosystems, when

a side-arm is cut off from the main river and a body of standing water is created (Amoros et al., 1987). Along with the eutrophication of the water body, growth of aquatic plant communities reduces the open water area and organic matter increases in the sediment. Herbaceous littoral plant communities follow, which are then replaced by *Salix cinerea* and ultimately by forest communities. This succession is another example for a positive feedback loop, as the settlement of one plant community (e.g. *Salix*) creates the conditions for a succeeding plant community by accumulation of biomass and evapotranspiration. This results in raised soil surface allowing forest communities to eventually establish. However, the natural succession can be reversed by floods, as nutrients and sediment are washed out, rejuvenating the eutrophic side arm. Ecosystems change constantly and oscillations between different states are reflected in community composition with implications for ecosystem processes and function.

How does self-organisation occur and what are its mechanisms? Ecosystems have to follow the laws of thermodynamics (Kay, 2000), whereas the first law of thermodynamics states that energy cannot be created or destroyed, so the total energy within a closed system stays the same, the second law states that entropy (disorder) should be maximised in a closed system. A simple experiment from physics illustrates the second law. When two containers, one filled with 1000 gas atoms and the other one empty, are connected, the system will move spontaneously towards its thermal equilibrium with 500 molecules in each and no gradient between the containers. This process is irreversible and also the state of maximum entropy. However, highly organised structures are observed in biology ranging from molecules to ecosystems, when the expected equilibrium state would be an even distribution of elemental particles. Schrödinger (1944) addressed this problem by recognising that living systems exist in a world of energy and material fluxes. Organisation is achieved by using energy from an outside system, reducing the entropy within, while increasing the entropy outside. Living systems, therefore, cannot be represented as closed systems, even in ecosystems that are sometimes regarded as closed systems, such as islands, lakes or ponds.

Non-equilibrium open systems are removed from thermodynamic equilibrium by energy and material fluxes across their boundary. Their form and structure (organisation) is maintained by dissipation of energy and they are known as dissipative structures (i.e. dissipative organisation; Kay, 2000). The theory states that they can exist for a prolonged time away from the equilibrium in locally-produced stable states when energy is supplied from outside (Prigogine, 1955; Nicolis, 1977). Convection, weather systems, living organisms, communities of organisms and ecosystems are examples of dissipative structures.

The Unified Principle of Thermodynamics (Kay, 2000) states that a system will resist being removed from the equilibrium state (a unique stable attractor) within a defined domain of attraction. If the system is removed from its equilibrium, then gradients are imposed on the system. As a consequence, the system will organise itself in such a way that reduces the gradients. Further increase of the gradient will trigger more sophisticated structures to oppose the movement away from equilibrium. This means that the system's ability to oppose the gradient increases the further away it is moved from equilibrium. The propensity of systems to resist being moved from equilibrium and to return to the equilibrium state when moved from it is referred to as the "Restated Second Law of Thermodynamics" (Kay, 2000).

The Restated Second Law of Thermodynamics can also be formulated in terms of "exergy", which is a further central concept of thermodynamics (Wall, 1986; Szargut et al., 1988; Bejan, 1997) and is a description of the quality of energy. Exergy is a measure of the maximum capacity of the energy content of a system to perform useful work as it proceeds to equilibrium and reflects all free energies associated with the system (Brzustowski and Golem, 1977). The presence of energy alone does not imply that it can be used, it is exergy that represents energy available to the system. During any chemical or physical process, energy looses exergy irreversibly. Exergy is a useful concept for studying non-equilibrium situations, since it serves as a measure of the distance that a system is from its equilibrium point - the larger the value for exergy, the further away the system is from equilibrium. If a system is exposed to exergy from outside, then it will be displaced from equilibrium. Again,

to degrade exergy as efficiently as possible, the system will organise itself, opposing further displacement. The further away a system has been moved from equilibrium, the more opportunities arise for more sophisticated organisation to be realised, hence the more effective the system becomes at exergy degradation (Kay, 2000).

In summary, dissipative systems exist in locally steady states away from equilibrium and are open to energy and material flows. The non-equilibrium state is maintained by imposed energy gradients (exergy) that, in return trigger self-organisation to oppose this gradient. As the system moves away from equilibrium, higher organisation occurs and more exergy is degraded. When the system's organisation increases, then more possible attractors become available. The system can shift suddenly when the present organisational structure does not dissipate exergy as efficiently as other available steady states. The process of energy and material cycling (positive feedback) is intrinsic to dissipative structures.

These concepts can now be applied to ecosystems. If earth is regarded as an open thermodynamic system with the sun imposing an exergy gradient, then dissipative structures will form. These can be physical, chemical or biological, e.g. oceanographic and meteorological circulation dissipate some of the incoming exergy, but also living structures have been shown to do so. Measurements of the surface temperature of terrestrial ecosystems show that more mature, complex ecosystems, such as forests, re-radiate energy at a lower exergy level than less complex structures, such as single species lawns (Luvall et al., 1990; Akbari et al., 1999). From an ecosystem point of view, one can state that biotic components act together in such a way that exergy degradation is maximised. With time, more complex organisation occurs, the diversity grows and the organisation becomes more hierarchical (Kay, 2000). In ecology, this phenomenon is known as ecological succession and Holling (1973) developed the adaptive cycle metaphor (Figure 2.1; Gunderson and Holling, 2002), whereby succession was regarded to be controlled by two phases: *i*) exploitation, which is defined by rapid colonisation of a recently disturbed ecosystem and dominated by r-strategists; and *ii*) conservation, which is defined by slow accumulation and storage of energy and materials and dominated by K-strategists (Gunderson

and Holling, 2002). The latter phase shows higher organisation and exergy degradation. Holling (1973) then added two more phases to this cycle dealing with "release" and "reorganisation" (Gunderson and Holling, 2002). Highly evolved and complex ecosystems become more fragile to disturbances, such as forest fires, insect pests and droughts, because biomass and nutrients are tightly bound. The release (also called "creative destructionism", Ω-phase) is followed by "reorganisation" (α-phase), where soil processes minimise nutrient loss, which are reorganised to be exploited by pioneer species. Transitions from r-phase to K-phase proceed slowly, whereas the other transitions proceed rapidly (Gunderson and Holling, 2002). Consider a pollution event in a stream that wipes out biota downstream of the pollution event (release). Reorganisation is initiated not through soil processes but through the constant supply of unpolluted water upstream of the event, which carries pioneer species with it. With the settlement of these pioneer species (r-phase) the possibilities for establishment of higher organisational structures emerge and K-strategists, such as fish, can re-establish and the system moves into the K-phase. The same can be applied to the floodplain example described earlier (Amoros et al., 1987). When the side-arm of a river is cut off (release), the created water-body retains nutrients (reorganisation), then eutrophication of the water-body allows pioneer plant species settle (r-phase), which are slowly replaced by more complex forest communities (K-phase). The system then re-enters the cycle when floods wash out nutrients and existing structures are destroyed (release).

2.3.2 Ecosystem integrity, resilience and stability

As discussed earlier, food webs are characterised by individuals interconnected by energy and material fluxes. Different trophic levels (i.e. primary production, consumption, and decompostation) are dependent on the type of resource being used, and the position of a species in a particular food web defines its trophic status (Dodds, 2002). Species composition is determined by abiotic factors (e.g. nutrient availability, temperature, flow), evolution and recently by the introduction of non-native species (e.g. Scheffer, 1990; Marchetti and Moyle, 2001; Scheffer et al., 2001;

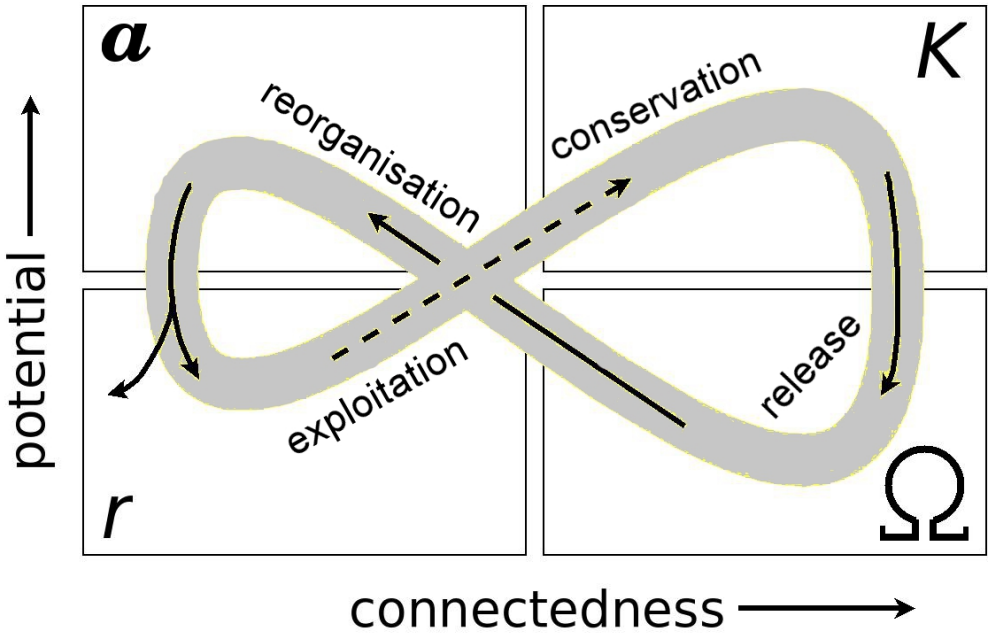


Figure 2.1: Holling's (1973) adaptive cycle. After Gunderson and Holling (2002).

Daufresne et al., 2004; Baxter et al., 2005; Davey and Kelly, 2007; Dewson et al., 2007; Mugisha and Ddumba, 2007). Therefore, different food webs are observed in changing conditions. Exergy dissipation may be the outside constraint that triggers forming of dissipative structures, but biota interact with their environment, influencing abiotic factors that consequently generate feedback loops. This is important because as a consequence species composition can influence the properties of an ecosystem as much as constraints from abiotic factors.

Especially with regard to ecosystem services, species composition is important to ensure desirable ecosystem function (Hooper et al., 2005). Riverine ecosystems are among the most heavily impacted natural systems (Sala et al., 2000), and it is pivotal to preserve the integrity and ensure high resilience of these ecosystems as they provide essential services (Costanza et al., 1997; Holmlund and Hammer, 1999; Wilson and Carpenter, 1999; Baron et al., 2002). The term of ecosystem integrity is strongly connected with a subjective human point of view of ecosystem services (De Leo and Levin, 1997). Webster's dictionary defines integrity as "the quality or condition of being whole or complete." The community structure is desired to support associated services (Cairns, 1977) and a healthy ecosystem should resemble a natural habitat that is expected for the region (Karr and Dudley, 1981). This definition calls for

a pristine ecosystem to compare other degraded ecosystems to. This is normally achieved by characterising structural and functional aspects and comparing systems to a hypothetical system in a pristine state. Impacts of disturbances can then be assessed and practical approaches to secure ecosystem integrity identified (De Leo and Levin, 1997). In context of Holling's (1973) adaptive cycle metaphor, a pristine system is not easily defined. Transitions between stability domains are a natural process, but with the recognition that some of these stability domains are less likely to supply desired ecosystem services, it might be less useful to use the terminology "pristine" system, but rather concentrate on the necessary processes that generate desired ecosystem services.

Resilience is a measure of the persistence of systems with multiple equilibria (Gunderson, 2000). A resilient system has the ability to absorb change and disturbances while the relationships between populations and state variables are maintained (Holling, 1973). The greater the change or disturbance that is required to transform a system from being maintained by one set of mutually reinforcing processes and structures to a different set, the greater is the resilience of a system (Figure 2.2). Resilience is embedded in the dynamic properties of an ecosystem. In other words: resilience is an emergent property of ecosystems over time and is influenced by the interaction of structure and process that create self-organisation (Gunderson, 2000). In physics and engineering, resilience is defined differently as the ability to quickly return to a previous condition. In ecology, the ability of a system to return to its original state after a temporary disturbance is called stability (Holling, 1973). The faster the system returns and the less fluctuations are expressed, the more stable the system would be (Figure 2.2). Stability is a measure of persistence for a system with one global equilibrium and the measure of stability is the 'return time' to that equilibrium. In summary, the choice of the measure to use depends on the type of question investigated. Stability can only be investigated close to one equilibrium point, to which the system state returns after a disturbance. Resilience can be applied to systems with multiple equilibria and measures the amount of disturbance a system can absorb before a system shift occurs. In the previous examples, stability

and resilience were defined for a stability domain that is fixed. The shape of the stability domain is defined by the chosen key variables, such as nutrients (Scheffer et al., 1993; Carpenter et al., 1999), species composition (Walker et al., 1997, 1999) or trophic relationships (He et al., 1993; Schindler et al., 1993). Those key variables can change over time (Figure 2.3) and this is called adaptive capacity.

The terms stability and resilience have been used ambiguously in the literature (Holling, 1973; Grimm and Wissel, 1997; Gunderson, 2000). In a review of the use of these terminologies, 25 definitions for stability and 17 for resilience were found (Grimm and Wissel, 1997). Altogether, 163 definitions from 70 different stability concepts and more than 40 measures were identified. Grimm and Wissel (1997) argue against the use of the term stability because of the many ambiguities and suggest to rather discuss stability properties than stability itself. Furthermore, Grimm and Wissel (1997) stressed that ecological systems are complicated and the concepts of stability and resilience have been developed for well defined, simple dynamic systems. Berryman (1991) disagreed with this view, and took the position that ecological systems obey the same rules as all other dynamic systems. In summary, the confusion over stability measures in ecosystems seems to be less due to the complicated nature of ecosystems, but more to the arbitrary use of stability concepts.

Resource based systems like forests or fisheries are sought to be kept in a state that guarantees optimal exploitation. This is also known as imposed resiliency (De Leo and Levin, 1997). Dynamic processes are thought to assure ecosystem function, so the resilience of a system to change over time is embedded in its heterogeneity and dynamic properties (DeAngelis, 1980). A high biodiversity seems to promote resilience and integrity (Hannah et al., 2005). Ecosystem resilience (in the sense of their reliability to provide goods) and the relationship to biodiversity has been considered based on concepts from reliability engineering (Naeem, 1998). In engineering, the more complex a machine, the more unreliable it becomes, but the redundant parts enhance its reliability. Naeem (1998) defined ecosystem complexity as the number of functional groups, and redundancy is expressed as high species richness within a functional group. Theoretical relationships of biodiversity and re-

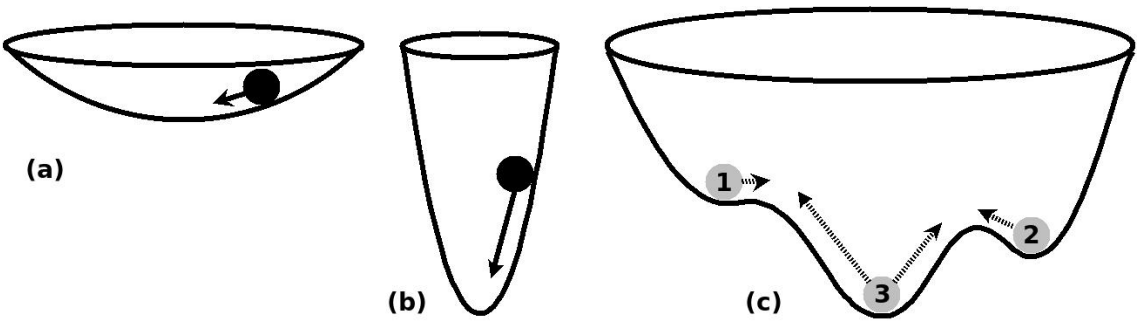


Figure 2.2: Difference between ecological resilience and stability (engineering resilience). The stability domain, which is defined by the shape of the cups, is fixed over time. The ball represents the system state. System (a) and (b) are examples of systems with different stability. Stability is defined by the slope of the cup. When the ball is removed from equilibrium (lowest point of the cup) return time will be faster in system (b) than in (a) and fluctuations will be higher in system (a) than in (b). System (b) is the more stable system. System (c) illustrates resilience. There are three locally stable states displayed (multiple equilibria). State 1 is the least, state 3 is the most resilient. Only a small disturbance will shift the system state from state 1 into state 3, whereas a larger disturbance is needed to shift the system state from state 3 into state 2. The amount of disturbance that is needed to shift the system state is illustrated by the length of the dotted arrows.

silience have been proposed by several authors (Naeem, 1998; Figure 2.4). These proposed relationships basically cover all possible relationships, from non-linear relationships (non-linear and hump-shaped), chaotic relationships (idiosyncratic) and monotonically increasing relationships (rivet-popping, compensating/keystone and redundancy).

According to Holling (1973), ecosystems in the K-phase (Figure 2.1) are less resilient than ecosystems in the r-phase (Gunderson, 2000; Gunderson and Holling, 2002). Riverine ecosystems are constantly exposed to change (e.g. floods, droughts), so maturity is rarely reached, except when side-arms are cut off, allowing the possibility of forest communities to develop. Constant disturbances also mean that the system can shift into another domain of attraction during reorganisation phase, which is the most vulnerable of the four phases. Change in abiotic factors can be followed by species loss or establishment of new species, which can have profound impacts on ecosystem structure and function (e.g. Paine, 1969b; Mugisha and Ddumba, 2007). The underlying concepts are discussed in the next section.

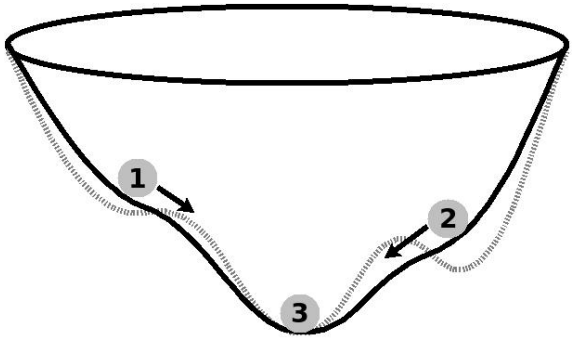


Figure 2.3: Adaptive Capacity. The shape of the cup (stability domain) is defined by key variables, such as nutrients, species composition or trophic relationships. When those key variables change, states that where previously locally stable (states 1 and 2) can become unstable. The grey dotted line shows the original shape of the stability domain with three equilibrium points. After the change (black, solid line) only one equilibrium remains (state 3).

2.3.3 The trophic cascade and keystone species

The composition of a community is controlled by bottom-up and top-down processes. The top-down control is also called "trophic cascade" (Carpenter and Kitchell, 1996). The bottom-up theory states that "a lot of prey can feed many predators" (Lampert and Sommer, 1999) and the biomasses on the adjacent trophic levels are positively correlated. The top-down theory states that many predators do not leave much prey, resulting in negative correlation of adjacent trophic levels. Both theories are not contradictory and there is evidence for both: observations in lakes give contradictory results in regards to biomanipulation experimentation. Fish species removal or introduction support the top-down theory, whereas comparisons of lakes at different trophic status support the bottom-up theory (Lampert and Sommer, 1999; Schwoerbel, 1999). Therefore, it is likely that both mechanisms act on the ecosystem, but which one elicits the more obvious effect depends on the type of ecosystem. Studies suggest that the cascade strength varies greatly among and within ecosystem types (Strong, 1992; Polis et al., 2000; Shurin et al., 2002; Hall et al., 2007). Mechanisms that are viable to cause a stronger cascade have been suggested and these include: differences in body-size among plants and herbivores (Shurin et al., 2002), higher mass-specific production rates (body size hypothesis; Shurin and Seabloom, 2005) and systems with more efficient herbivores (herbivore efficiency hypothesis;

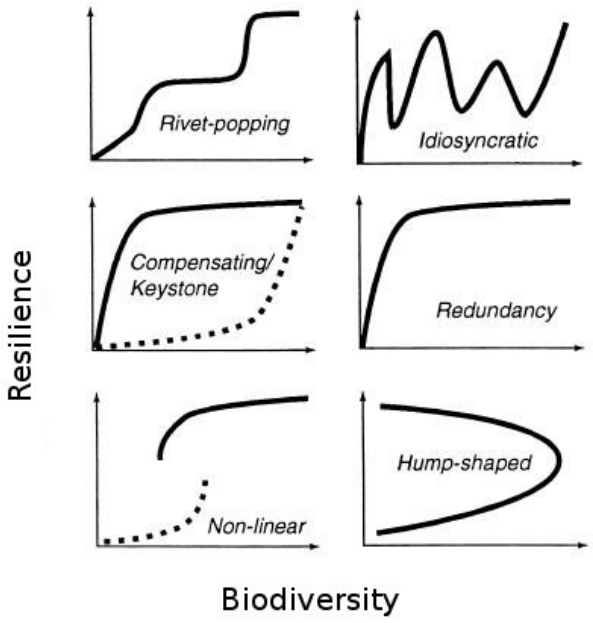


Figure 2.4: Theoretical relationships of resilience and biodiversity after (Naeem, 1998, Figure 1). The following authors proposed the different relationships: rivet-popping, (Ehrlich, 1981); non- linear, (Carpenter, 1996a); redundancy, (Walker, 1992); (Lawton, 1993); idiosyncratic, (Naeem et al., 1995); humped-shaped, (Rosenzweig, 1993); and compensating/keystone, (Sala et al., 1996).

Strong, 1992; Polis, 1999; Borer et al., 2005). Polis et al. (2000) summarised the difficulties involved in defining meaningful measures of trophic cascades with his statement: "Like good artwork, most ecologists would recognise (and agree on) a trophic cascade when they see one". A traditional measure for a trophic cascade is a change in plant biomass which also can be taken as a measure of productivity (Polis et al., 2000) and another possible measure could be a change in plant community composition (Schmitz, 2006). The question that arises for both measures is how much change is defined as a trophic cascade? Statistically significant results might not be biologically meaningful. With a terrestrial ecosystem, Schmitz (2006) found only modest top predator effects on community properties, but strengthening effects on ecosystem properties, as plant species evenness was enhanced in presence of the top predator.

The magnitude of the effect one species exerts on another species' abundance is expressed as interaction strength. Recent studies indicate that the interaction strengths among species in a food web are skewed, rather than symmetrically dis-

tributed (Berlow et al., 1999; Berlow, 1999). Few species have a high interaction strength (exertion of a strong effect on the abundance of other species), whereas most have weak or no detectable effects (Berlow, 1999; Emmerson and Raffaelli, 2004). Patterning of interaction strength could have consequences for food web stability and, consequently, community and ecosystem stability (Emmerson and Raffaelli, 2004). Emmerson and Raffaelli (2004) also found that body size of predators and prey could be used to predict interaction strength (in this case measured as the log-ratio measure of interaction strength; Berlow et al., 2004). The term "interaction strength" is used ambiguously in ecology and there are different measures of link weight that are summarised with their advantages and disadvantages by Berlow et al. (2004). The main distinction of these measures is the scale they are being used on (property of individual link or whole system response). The absolute change in biomass, or abundance respectively, for any species, as a response to a change in another species abundance is called "absolute prey response" and characterises visually dominant effects. It is a whole system response measure. Further measures include the inverse interaction matrix (Bender et al., 1984; Yodzis, 1988), secondary extinctions (Borrvall et al., 2000; Sole and Montoya, 2001; Dunne et al., 2002b) and log-response ratio (Laska and Wootton, 1998; Berlow et al., 1999). Trophic cascades have been shown for terrestrial, marine, and freshwater systems (Power, 1990; Huryn, 1998; Shurin et al., 2002; Knight et al., 2005), but they seem to be strongest in lentic freshwater systems (Shurin et al., 2002). The reason for this finding might be that lentic freshwater systems are relatively shut off from migration. The magnitude of prey exchange strongly influences predator effects on prey, as a comparison of exclusion experiments that used cages with different mesh sizes showed (Cooper et al., 1990). Small mesh sizes hindered prey exchange and higher predator impact was measured than in cages with larger mesh size. Predator impact can also be altered by the presence of a second predator (Worsfold et al., 2009), predator identity and predator species richness (Nilsson et al., 2008). Effects of trophic cascades can propagate across ecosystems, e.g. fish indirectly facilitate terrestrial plant pollination in the vicinity of ponds by preying on dragonfly larvae and as a consequence less

adult dragonflies emerge, which prey on insect pollinators (Knight et al., 2005). In summary, the strength of trophic cascades depends on the combination of ecosystem, community, and species characteristics.

Single species that elicit a trophic cascade when they are removed and consequently alter community composition (e.g. by changing plant biomass or affecting biodiversity) are often referred to as keystone species. Like an arch, which is held upright by its keystone, a keystone species is important for community stability. Originally, Paine (1969b) defined a keystone species as "a species of high trophic status whose activities exert a disproportionate influence on the pattern of species diversity in a community". The term "keystone" was used as a metaphor rather than as the postulate of a new concept (Hurlbert, 1997), although currently, the term keystone is used widely and triggers many proposals for new definitions of the concept (Lamont, 1992; Bond, 1993; Mills et al., 1993; Paine, 1995; Power and Mills, 1995; Folke et al., 1996; Power and Tilman, 1996; Piraino et al., 2002; Davic, 2003). A keystone species does not have to be a predator, but may be any species with a large effect on any aspect of ecosystem function. This led to terms like keystone-prey, -competitor, -mutualist, -disperser, -pollinator, -earth-mover, -habitat modifier, -engineer, -host, -processor, -plant, and -resources, or keystone functional groups. The keystone concept is not without criticism. There is a lack of evidence of empirical or theoretical foundation for the existence of a natural dichotomy, which corresponds to the verbal distinction of keystone vs. non-keystone Hurlbert (1997). However, the concept is useful to assess a species' ability to add stability to a food web and has gained much interest for targeting conservation efforts efficiently (Power and Tilman, 1996; Jordan, 2009). To be used efficiently, keystone effects need to be quantified, as assessments need to be objective and predictive (Jordan, 2009). One aspect in the identification of keystone species is the connectedness of the species nodes. For example, the lower trophic level of 'wasp-waist'-like communities is connected to the higher trophic level by only one (or very few) species, which make them energy gateways (Cury et al., 2000). The loss of this wasp-waist species would cause a reorganisation of energy pathways and ecosystem regime shifts (Jordan et al., 2005). Wasp-waist species are

often very abundant (Jordan et al., 2005) and, consequently, they are not of primary concern, since conservation efforts are often directed towards rare species.

For water courses, the following keystone species have been identified: Power (1990) found that in the presence of fish that prey on predatory insects and fish fry, filamentous green algae are reduced to low, prostrate webs, infested with chironomids. In fish-less exclosures, the smaller predators control chironomids, algal biomass is high and the algal turf is covered with diatoms and cyanobacteria. Not only algal biomass can be affected by predator prey interactions on higher trophic levels, Woodward et al. (2008) identified European bullhead (*Cottus gobio*) as a keystone species of a small chalk stream. In the investigated stream, the fish assemblage is dominated by *C. gobio* and exclosure experiments revealed strong negative impacts on two prey species- the detrivore *Gammarus pulex* and the algal grazer *Potamopyrgus antipodarum*. Whereas detritus processing rates were suppressed in cages containing *C. gobio*, algal production did not differ (Woodward et al., 2008), so the trophic cascade acted on the detrital energy pathways. Consequently, other aspects of ecosystem function than plant production should be considered as well when searching for keystone species.

The main question remains: How can trophic cascades and system regime shifts be quantified in an objective and predictive manner? Owing to the different ways keystone species can induce a regime shift, it is possibly best practise to assess a combination of measures, such as changes in biodiversity, production, structural aspects of the food web (e.g. connectivity and link density), secondary extinctions, and dynamical aspects (e.g. energy cycling).

2.4 Biodiversity effects on ecosystem services and stability

The consequences of declining biodiversity on ecosystem services and stability[1] have become of great interest in the background of accelerated species loss (Duffy, 2002). In the 1950s, the view that more complex communities are more stable was developed. Evidence from agricultural monocultures and simple island communities indicated that these systems were highly vulnerable to invasions when compared to complex mainland communities (MacArthur, 1955; Elton, 1958). Elton (1958) formulated the diversity-stability hypothesis, which states that increased biological diversity leads to greater ecological stability and predictability and MacArthur (1955) linked increased stability to an increase in the number of species links, which is more likely in diverse communities. By the end of the 1950s, the positive correlation of stability and biodiversity was treated as ecological theorem (Hutchinson, 1959). Although supported by experimental findings (e.g. King and Pimm, 1983; Tilman and Downing, 1994; McGradySteed et al., 1997; Naeem and Li, 1997), the theory was seriously challenged by the analytical work of May (1972, 1973), who found that an increase in number of species and links between them decreases stability when the nodes are randomly connected (May, 1972). Hence, biological diversity and complexity were not guarantors for stability, and other mechanisms and structures, which May (1973) termed "devious strategies", had to be found to explain the observed diversity and complexity of ecosystems. However, natural food webs are not connected randomly, but elicit small world behaviour, i.e. they are generally highly clustered with short path length between species and the distribution of links is skewed (Montoya and Sole, 2002). Further food web topology studies demonstrated the non-randomness of ecosystems (e.g. Williams and Martinez, 2000; Dunne et al., 2002a, 2004) and increased stability of empirically consistent food webs (Martinez et al., 2006). Omnivory might be destabilising (Pimm and Lawton, 1978) or stabilising (McCann and Hastings, 1997) and weak interactions, if the are

[1]The term stability is used in this section in its broadest sense, combining ecological and engineering resilience in its meaning, if not stated otherwise.

predominant, might stabilise complex communities (McCann et al., 1998). Two sets of three species food chains that were linked by the same top predator could be stabilised, when the top predator was allowed to switch preferences for its prey species (Post et al., 2000). Furthermore, with the number of trophic levels, the frequency of chaotic dynamics increases, but decreases with other stabilising structural properties (Fussmann and Heber, 2002).

Although biodiversity seems to be positively correlated to ecosystem stability, it is not essentially the driver of stability and this correlation does not necessarily extend to stability measured on the population level (McCann, 2000). Diverse communities potentially contain species that survive environmental disturbances and compensate for reduced competitors (Loreau and Behera, 1999), consequently, diverse communities are potentially better 'insured' against environmental change and able to sustain ecosystem dynamics in uncertain environments (Elmqvist et al., 2003). Diversity is measured in two dimensions: functional and response diversity. Functional diversity refers to the diversity of functional groups within an ecosystem (Elmqvist et al., 2003). Loss of functional diversity can alter ecosystem states, e.g. loss of the top predator (or top predator guild) can elicit a trophic cascade (Carpenter and Kitchell, 1996) and functionally diverse ecosystems have been found to be less sensitive to invasion (Stachowicz et al., 1999; Chapin et al., 2000; Knowlton, 2001). Response diversity refers to the concept of redundancy within functional groups (Elmqvist et al., 2003). Although members of a functional group may perform the same function, their response to disturbances might be quite different. A reduction of response diversity therefore leads to a less resilient ecosystem. For example, detrivorous macroinvertebrates in streams are affected differently by pollution. Crustaceans are sensitive to stream acidification, but tolerant to organical pollution, whereas plecopterans are affected contrary (Woodiwiss, 1964; Dangles and Guerold, 1999). Without this insurance, the process of leaf litter breakdown would stop in the case of pollution, with consequences on higher levels of the food web, since detritus is an important energy pathway in freshwater streams (Newman, 1991; Moore et al., 2004). Interestingly, it has also been found that the leaf litter breakdown rates were

higher than expected, when shredders were cohabited, compared to isolation (Jonsson et al., 2002). These results suggest not only the presence of response diversity, but also functional diversity. Although the macroinvertebrates used for the experiment were all shredders, their efficiency varied and in cohabitation they seemed to complement each other. Similar results have been found for plant communities (Walker et al., 1999) and coral reef communities (Hughes, 1994). Functional diversity increases performance, since resources can be exploited more efficiently, whereas response diversity is important to maintain ecosystem processes after perturbations (Elmqvist et al., 2003). Consequently, slow erosion of response diversity may not only reduce resilience, but also functionality.

In the vulnerable stage of reorganisation (Figure 2.1), response diversity might be one of the key factors determining whether or not the system shifts towards a new domain of attraction, which is potentially characterised by ecosystem processes that do not support desired ecosystem services (Chapin et al., 1997). In the exploitative phase and conservation phase, when ecosystems deliver desired services, regime shifts seem to be less likely under conditions of high biodiversity and extensive omnivory (Pace et al., 1999). The stabilising effect of weak interactions on complex communities (McCann et al., 1998; Neutel et al., 2002) could be negatively influenced by biodiversity loss because of accompanying loss of weak interactions and shift towards preponderance of strong, destabilising interactions (McCann, 2000). In summary, biodiversity does increase stability in non-randomly interacting communities.

In the last decade, the relationship between biodiversity and ecosystem services received growing attention, but small-scale and highly controlled experiments over short time-periods often lack relevance to natural ecosystems and realistic extinction scenarios (Duffy, 2009). In general, biodiversity enhances ecosystem function, specifically when the focus lies on the provision of more than one ecosystem function or service (Reiss et al., 2009). The biodiversity-ecosystem function relationship is not simple and two mechanisms, 'selection effect' and 'complementarity effect' have been proposed to operate in combination. In the selection effect, species dominance affects ecosystem processes positively or negatively according to the domi-

nant species' specific traits, whereas the complementarity effect is always positive and leads to increased total resource use by resource partitioning or positive interactions (Walker et al., 1999; Loreau and Hector, 2001; Jonsson et al., 2002). The complementarity effect is predicted to emerge over time (Pacala and Tilman, 2002), which is confirmed in long term experiments and, simultaneously, the number of species required to maximise function increases (Tilman et al., 2001; Hooper and Dukes, 2004; Cardinale et al., 2007; Stachowicz et al., 2008). Dominant species tend to influence ecosystem processes strongly (Grime, 1998; Polley et al., 2007), and few species are needed to maintain normal ecosystem function. For example, a common finding in experiments is that ecosystem function saturates at a species richness level lower than that found in nature (Schwartz et al., 2000). Monocultures can produce higher yields (e.g. crops, aquaculture) and, at the same time, are harvested more efficiently (Folke, 2003; Duffy, 2009). In these systems, the focus is on a single response variable, such as plant or fish biomass accumulation, but even when a single species dominates a specific ecosystem service, it is unlikely to also dominate other processes of interest. Indeed, as the considered number of ecosystem services increases, redundancy among species decreases and the relationship between species richness and (multivariate) ecosystem function grows stronger (Petchey and Gaston, 2002b). This phenomenon is termed 'multivariate complementarity' (Duffy et al., 2003; Bracken and Stachowicz, 2006; Hector and Bagchi, 2007; Gamfeldt et al., 2008). Moreover, rare species can make important contributions to ecosystem processes under changing conditions (Lyons et al., 2005). It has been suggested that the influence of diversity increases in heterogeneous conditions (Tilman et al., 1997; Cardinale et al., 2000; Loreau et al., 2003), but most biodiversity - ecosystem function experiments have been conducted in small plots, under highly controlled, homogenised conditions (Duffy, 2009). Cardinale et al. (2005) found that the relationship between primary producer diversity and productivity in stream ecosystems varies according to the disturbance history, suggesting that ecosystems that are characterised by disturbance and high variability are more sensitive to biodiversity loss. Additionally, the maintenance of local biodiversity at a certain level requires a

larger number of species at the regional scale (Duffy, 2009). Species loss negatively affects ecosystem function, if extinction scenarios are realistic and non-random (Jonsson et al., 2002; Petchey and Gaston, 2002a; Ostfeld and LoGiudice, 2003; Solan et al., 2004; Zavaleta and Hulvey, 2004). It has also been suggested that bottom-up and top-down processes might be stronger drivers of ecosystem services than biodiversity effects. For example, an increase in resource abundance can intensify competition and as a consequence reduce diversity (paradox of enrichment; Huston, 1997). Contrary, the few available experimental data suggest that changing diversity within trophic levels has non-trivial consequences, even within the context of dynamic ecosystems impacted by other factors (Duffy, 2009). For example, changes in species richness of herbivorous pond snails, had comparable or greater effects on a range of ecosystem processes than nutrient supply or predator exclusions (Wojdak, 2005). Restoration of biodiversity in marine environments increased productivity of fisheries and, generally, highly diverse ecosystems provided more services with less variability (Worm et al., 2006).

The evidence suggests that stability and ecosystem services are linked to biodiversity, however, in both cases, biodiversity is not the only driver. The influence of biodiversity on ecosystem services is strongly dependent on the environmental context and on the amount of desired ecosystem service. Consequently, assessments of biodiversity alone do not permit to draw conclusions about ecosystem function and stability.

2.5 Conclusion

The maintenance of healthy ecosystems, which consistently provide ecosystem services and functions even in the background of environmental change, appears to be strongly connected to the preservation of natural, diverse and dynamic communities. While ecosystem services are maintained, community compositions can be highly variable, so the recognition of alternative domains of attraction (e.g. defined by the ecosystem services that are provided) and drivers that cause system shifts

pose invaluable information for ecosystem management and conservation. Species interact in a food web context and the structure and dynamics of these interactions determine the type of ecosystem services provided and the ecosystem stability. Therefore, the study of dynamic food webs, theoretically and empirically, gives important insights into ecosystem function and consequences of disturbances.

Although ecosystem theory seeks to identify general patterns that are valid across different types of ecosystems, ecosystem-specific dynamics should be the focus for predictions regarding the response to disturbances and environmental change. The design of predictive food web models should have close resemblance to the investigated system, because randomly assembled food webs can posses properties not observed in nature. Furthermore, the decisions made in order to build food web models will have consequences on its behaviour. When investigating the impact of disturbances on food webs, the type of disturbance, the response variable and a reference state or dynamic have to be defined and spatial and temporal scales need to be considered. Natural disturbances tend to be pulsed, whereas human induced disturbances are often prolonged or chronic (Bengtsson et al., 2003). And in food webs that are often subject to predictable disturbances, organisms will have evolved to benefit from those disturbances, compared to more stable ones (Marchetti and Moyle, 2001). The definition of a reference state tends to be more difficult, as response variables (e.g. species abundance) tend to fluctuate naturally over time and a decision has to be made whether or not the system has shifted into a different domain of attraction after a disturbance. Thought has to be given to the level of description. When the objective is to understand ecosystem or community level dynamics, several trophic levels should be included into the food web model. This poses difficulties with regard to consistent resolution, as empirical data upon which the model should be built, often shows higher resolution at the higher trophic levels, whereas species are aggregated at lower trophic levels. Assessment of biodiversity effects is made difficult with species aggregation, but is important with regard to the current loss of biodiversity. Specifically, the interdependence of community composition, species traits, food web dynamics and ecosystem services needs further investiga-

tion. Desired ecosystem services could serve as an objective function, for example, if the objective is to maximise one service, e.g. aquaculture production, then solutions could be achieved easily with less diverse systems. But if several ecosystem services are of interest (e.g. regulation of ecosystem resilience, food production, nutrient recycling), then diverse communities maximise multiple properties simultaneously and further knowledge of food web dynamics, structure and the consequences for ecosystem function are required.

Chapter 3

The aquatic food web model: River Frome

3.1 Introduction

Fresh waters are currently subjected to numerous impacts, such as eutrophication, climate change, toxic pollution, acidification, non-native species, over-harvesting and habitat destruction (Covich et al., 2004). These threats can have profound consequences on their ability to deliver important goods and services (Covich et al., 2004; Woodward et al., 2005a; Balvanera et al., 2006; Schindler, 2007). How environmental stressors affect ecosystem services is determined by ecosystem resilience, which is thought to depend on biological organisation (*cf.* Chapter 2). Food webs describe communities with the focus on trophic interactions (predator-prey relationships), with nutrient recycling and energy fluxes through the ecosystem dependent on these interactions (e.g. DeAngelis, 1980), along with population and community dynamics Shurin et al. (2002). Thus food web research has developed into a central issue in ecology (de Ruiter et al., 2005). Because of the interrelationship of community dynamics and ecosystem function, food web analysis provides a solid approach to assess impacts of environmental change (Ings et al., 2009). Those impacts cannot be completely understood if the investigated system contains only one trophic level or only

single predator-prey interactions are studied, since multilevel food webs can produce complex behaviour and responses to disturbances can be counter-intuitive (Wilbur, 1997; Thebault and Loreau, 2003; Woodward, 2009; Woodward et al., 2010). Emergent behaviours, such as resilience and ecosystem function, can only be investigated if the system is studied at higher levels of organisation (e.g. food web or ecosystem level). On lower organisational levels (e.g. population, single trophic level, single predator-prey interactions), research can add to the understanding of the functional parts of the system, but are inadequate to draw predictive conclusions to ecosystem function and, ultimately, ecosystem services.

Food webs can be described qualitatively and quantitatively. Topological models are a qualitative description of food webs (i.e. "who eats whom?") with variables of interest, such as connectance (number of links), and the focus is on food web patterns and how these patterns influence food web stability (Dunne et al., 2002b; Montoya and Sole, 2002, 2003; Ings et al., 2009). Dynamical models consider the amount of material and energy flow over time (De Ruiter et al., 1998; DeRuiter et al., 2005). They are a quantitative description of the system, useful to generate predictions of changes in species abundance and test system behaviour to disturbances. Dynamical models normally consist of a set of differential equations that characterise the relationships between the defined compartments (e.g. species, functional groups). The Lotka-Volterra model, developed independently by Lotka (1925) and Volterra (1926), is the simplest of the predator-prey models and is based on two-species-interactions. Dynamic multi-species models can capture feedback loops and, therefore, emergent properties that cannot be seen in linear systems, but they depend strongly on the quality of the input parameters in their ability to make predictions (e.g. Baird et al., 2009).

The alteration of food web dynamics (e.g. through loss or addition of species, change of processing rates), can have impacts on ecosystem function, such as primary and secondary production (Polis et al., 2000; Schmitz, 2006). How stressors impact on biological organisation (e.g. populations, communities, food webs or ecosystems) is still far from understood. Studies of multi-species assemblages across different

trophic levels are especially rare (Woodward, 2009). For example, theoretical approaches that investigate the relationship of biodiversity and ecosystem function are ahead of available data (Thebault and Loreau, 2003, 2005, 2006). However, without empirical evidence, theoretical models might not possess sufficient reality. In the present study, this gap is attempted to be bridged by developing a food web model based on empirical data to analyse impacts of stressors on biodiversity and ecosystem processes (Chapters 4 to 6). To do so, a dynamical approach was chosen in order to be able to capture processes.

Aim and objectives

The aim of this chapter is to develop a dynamical food web model based on data from an English, temperate chalk stream, which will serve as the Baseline Model that will be manipulated in the consequent chapters to assess the impacts of a range of environmental changes.

Objectives are:

1. Establish species abundances from empirical data.
2. Establish diet compositions from literature.
3. Establish feeding rates.
4. Develop Baseline Model that closely resembles the natural community.

3.2 Material and Methods

3.2.1 Study site

The selected study site was a chalk stream in Southern England. Chalk streams are a special type of calcareous stream found where chalk emerges on the surface of the earth. Rainfall drains slowly downwards through the highly porous chalk until it reaches an impervious layer below the chalk, where it accumulates, forming an aquifier. Chalk streams rise where those aquifiers reach the surface, and their flow originates mainly from ground water with little influence from surface runoff. The annual hydrograph is characterised by an increasing discharge during the winter, when the aquifiers rise and a decreasing discharge during the summer, when low precipitation does not fill the aquifiers and they slowly empty. Normally, a substantial increase in discharge can be observed in December and continues until March and April. In dry winters, the aquifiers do not rise as much and the effects can be observed as low discharge during summer. Low discharge exerts several ecological effects on chalk streams, as silt accumulates and affects the growth of macrophytes, changes the macroinvertebrate community, and influences the spawning success of salmonid species (Berrie, 1992).

Another notable characteristic of chalk streams is a relatively stable temperature in comparison to streams that are less influenced by ground waters. Spring water from aquifiers in southern England emerges at about 11°C, warming the water in winter and exhibiting a cooling effect in summer. Hence, water temperature rarely falls below 5°C and rarely exceeds 17°C. The effect of the spring water decreases in the lower reaches, and in prolonged periods of high temperatures (Berrie, 1992).

The chemical composition in chalk streams also remains fairly constant, and the main nutrients for plant growth (nitrate, phosphate, potassium, and silicate) are abundant and normally do not fall below a level where they would limit plant growth. The combination of high level of nutrients and stable flow offers ideal conditions for the growth of aquatic plants, such as epilithic algae and macrophytes. Annual net

production of epilithic algae has been reported as 76–124 g organic matter per m^2 (Marker, 1976).

The dominant macrophyte in chalk streams is *Ranunculus spp.* but many higher plants flourish in the chalk stream environment and growth patterns of the macrophyte community show seasonal characteristics (Ham et al., 1981, 1982). Production of *Ranunculus spp.* can reach about 400 g m^{-2} dry weight but is normally around 200 g m^{-2} dry weight. Chalk streams receive most of their energy as allochthonous input (Westlake et al., 1972; Dawson, 1976; Hynes, 1983), but because of the high primary productivity they are thought to be less dependent on this than other small streams (Berrie, 1976). However, allochthonous input is the main pathway energy enters the food web, since few macroinvertebrates feed on living macrophytes (Newman, 1991; Pinder, 1992).

Chalk stream fish communities are diverse, and individuals tend to be fast growing, especially brown trout (*Salmo trutta*), due to ideal temperatures and abundant food. Chalk streams are important for angling, watercress production, and their course and structure has been altered to improve farmland and to drive water mills. Chalk aquifiers provide high quality water, but abstraction has led to a serious reduction in discharge (Berrie, 1992).

The River Frome, Dorset, is a typical medium sized chalk stream in Southern England (Crisp and Westlake, 1982), rising near Evershot and entering the English Channel at Poole Harbour. Mean monthly temperatures range from 6.5°C in winter to 17.4°C in summer, and the pH is slightly alkaline (7.5–8.5). Water quality is good to very good (River ecosystem classification 1 and 2) and the river is classified as a UK Biodiversity Action Plan chalk stream habitat (Knight, 2006). The food web model is built from quantitative and qualitative long term data collected in the Millstream, a tributary of the River Frome that is considered as a smaller and shallower version of the main river (UK national grid references SY867863 to SY898862; Figure 3.1). This is reflected in its nearly identical species communities, for example fish and macroinvertebrates. The Millstream separates from the River Frome

near East Stoke and the surface area for a 200 m stretch is approximately 1200 m^2 (Knight, 2006). The surrounding area is used extensively as pasture for cattle. The riverbed is characterised by a gravel and sand substrata supporting abundant growth of *Ranunculus spp.* in summer. The combination of high water quality and chalk stream habitat supports high biological productivity in the river. The food web of the Millstream comprises trophic links between fishes, macroinvertebrates, macrophytes, detritus and other microorganisms (Fig. 3.2).

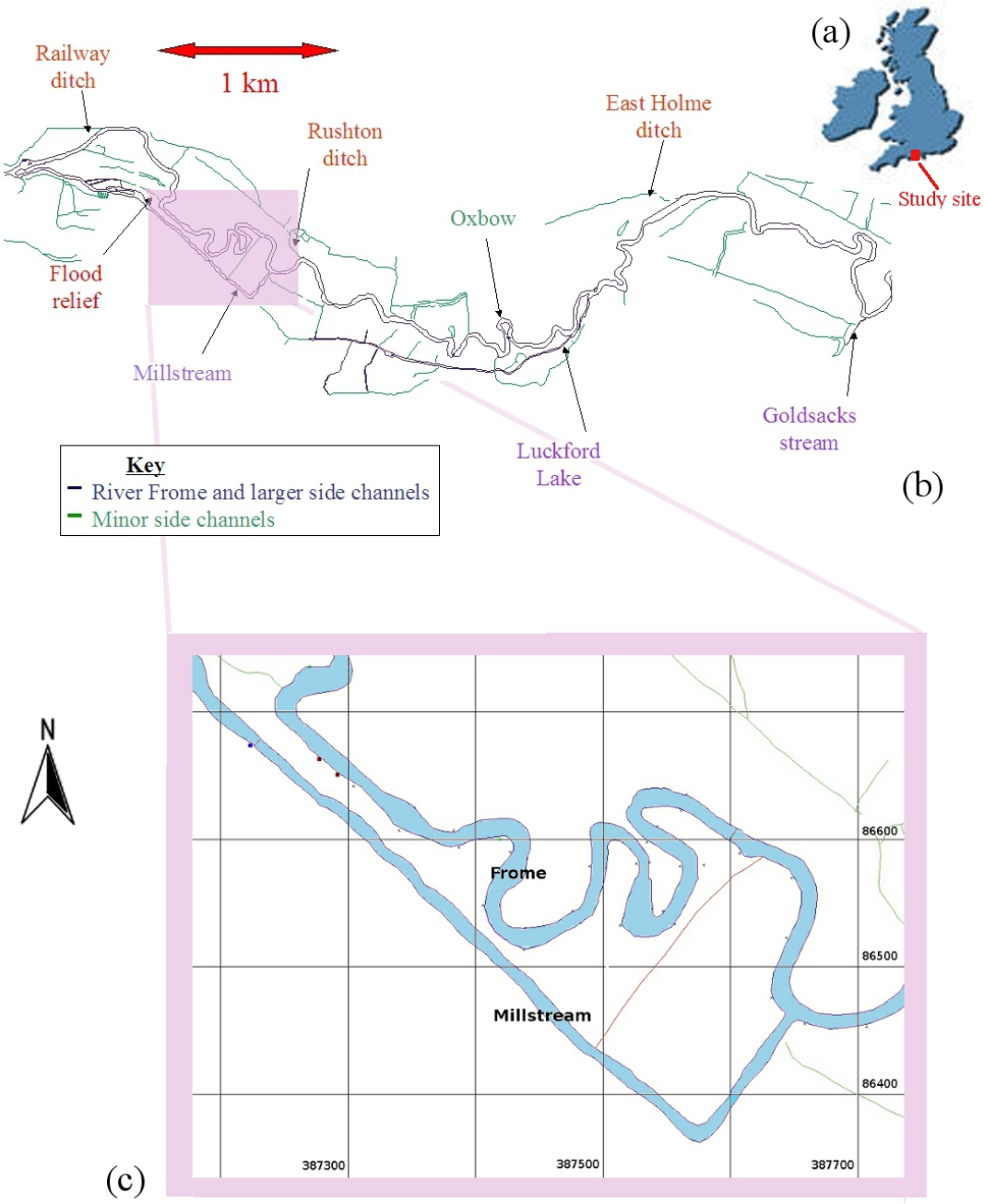


Figure 3.1: (a) Location of the study site in the UK; (b) aerial view of Millstream (Knight, 2006) and adjacent rivers; and (c) of the Millstream.

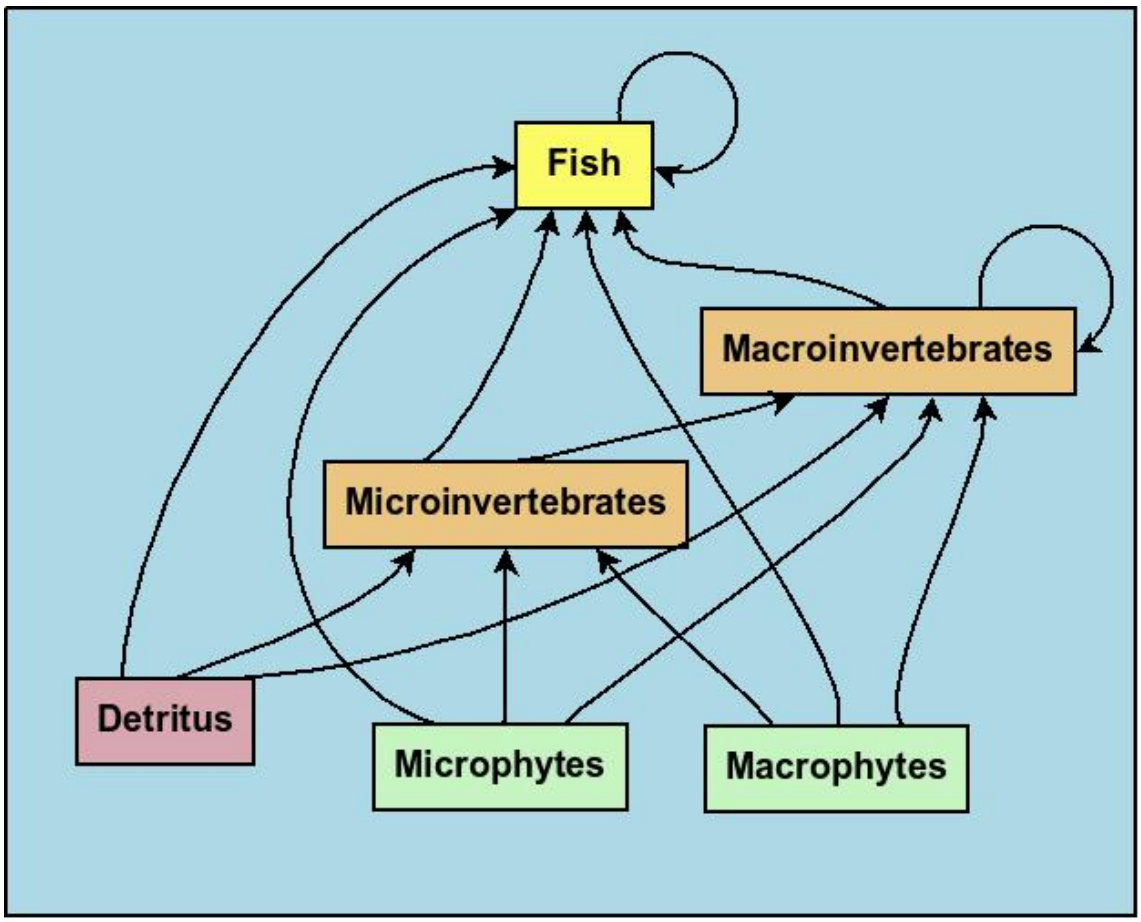


Figure 3.2: Schematic food web of the Millstream showing predation links among the main taxonomic groups. The arrows indicate the direction of energy flows. Micro- and macrophytes use dissolved nutrients and energy from the sun and detritus receives input from all compartments, but for clarity those flows are not depicted.

3.2.2 Aquatic food web model

The development of the Millstream food web required certain parameters for the chosen model to work. In general those were: *i*) some measure of abundance of the compartment (i.e. species) in the form of absolute numbers, biomass or energy per area to form the starting stock values; *ii*) information about how these compartments were connected (i.e. diet composition) to form the species links; and *iii*) information about the magnitude of energy flow between the compartments to characterise how many units were transferred from one compartment to another in a given time and space to form the energy transfer between species. To fulfil these requirements, a combination of empirical data from the River Frome and the diet composition of species derived from the literature was collated and processed to fulfil the demands of the modelling approach. In particular, the chosen modelling approach required energy values (cal) as the unit for the compartments, which were not readily available in the literature.

Collation of data

Fish species The empirical fish data set used to build the food web was collected by quantitative electrofishing sampling completed between 2003 and 2005 as part of the LOCAR (LOwland CAtchment Research) programme (`http://www.nerc.ac.uk/research/programmes/locar/`). Sampling was conducted four times a year in winter, spring, summer and autumn. The sampled stretch of the Millstream was 200 m long, and was divided into 50 m stretches for quantitative assessment of the fish communities. The 50 m sections were separated by 'stop nets' and electrofished using a three pass depletion method. The total area fished was 1200 m^2 (Knight, 2006). Captured fishes were identified to species level, and a sub-sample was measured for fork length (FL) to the nearest mm, and weighed to the nearest g. Species specific length-weight relationships were calculated and used to obtain biomass and energy values for the compartments used in the model (*cf.* Section 3.2.3). Complementary length-weight relationship were collated from the literature, as for some

species the number of samples taken did not produce a statistical reliable length-weight relationship ($r^2 < 0.9$, Appendix, Table A.1). In addition, diet compositions of the fish species were collated from the scientific literature, where extensive information for the Frome exists (Mann and Orr, 1969; Mann, 1971, 1976a,b, 1980a,b, 1982; Mann et al., 1989; Mann and Blackburn, 1991) and were transformed into feeding rates. Diet compositions were expressed as %-number, %-occurrence, or %-biomass and had to be converted into energy intake per day.

Macroinvertebrate species Two surveys using the British Monitoring Working Party (BMWP, Hawkes, 1998) methodology were carried out by the Centre for Ecology & Hydrology (CEH) between 2002 and 2005 and provided presence/absence and abundance characterisation of the invertebrate community of the study site. An additional survey was carried out for this study in 2008 to provide biomass estimates (g m^{-2}). Samples were collected by kick-sampling method. One survey provided abundance data identified to family level, whereas the second survey provided presence/absence data identified to species or genus. The fifty five species present from 2002 to 2005 were included in food web, although aggregated. Species frequencies provided by the second survey were used to estimates species abundance within families of the first survey. Finally, the 2008 survey provided data on densities (wet weight in g m^{-2}).

The 2008 survey was partly conducted by the author. A total of 36 samples were taken in different habitats (e.g. gravel, *Ranunculus* cover) at dawn, midday and dusk (12 samples for each time of day) on the 30th of July 2008 and the 28th of August 2008 using a standard sampler Surber (1 min), to ensure a robust estimate for mean biomass. The samples were kept in alcohol until the invertebrates were sorted from debris in the laboratory; excess fluid was dried off carefully with a tissue and the wet weight was measured. The invertebrates were not identified, but the mean biomass per m^2 was calculated from the area covered by the surber net (33 cm x 30 cm = 0.099 m^2; Table A.2).

3.2.3 Development of the dynamical model

Introduction of the dynamical model

The dynamic simulations of the food web were run with EcoNet, a simulation and analysis software developed at the University of Georgia (http://eco.engr.uga.edu; Kazanci, 2007). The model, written in text format, was entered into a web interface and then run on the external server. It was built from values for the compartments and the flow rates between those compartments (nodes). The following parameters were required by EcoNet to create the food web:

1. Names of nodes
2. Starting stock values for nodes
3. Flow rates between nodes

EcoNet handles simulations with two different modules. One converts the model into differential equations; the other solves the differential equation using a method and parameters that can be selected. The method determines how the differential equations were solved (*cf.* Appendix C.1). Analysis was run with the adaptive time-step method. Although ecosystems behave in a probabilistic manner, this method was chosen over the stochastic method because the results did not differ, and the calculations were solved faster with the adaptive time-step method. The parameter *Max Time Steps* set the duration of the simulation and was chosen so the final output could be assumed to be steady state. In steady state, the stock values did not change over time- and so the network "relaxed" into its final state. The parameter *Sensitivity* determined the accuracy of the numerical solution of the differential equations. Higher values were described to be less accurate, but trial runs with different *Sensitivity* values did not produce distinct results (*cf.* Appendix C.2). The solution consists of a network graph, the time-course of the compartment values and additional analysis, such as through-flow analysis, link density, connectance, and flows at steady state (http://eco.engr.uga.edu; Kazanci, 2007).

The data for fish species possessed higher accuracy with regard to abundance and diet composition than the data for macroinvertebrates. This was mainly due to the invertebrate data not being collected with the goal to establish a food web, but to assess biological water quality, and to diets of fish being easier to identify to species and therefore are better known than macroinvertebrate diets. For the dynamical model, macroinvertebrate species were organised into family groups. Although there were several ways in which species could be organised (e.g. trophic species, feeding guilds), families were used to present most diet compositions for fish in the literature, so this grouping was adapted. This grouping may not be the most intuitive, since families contain species with different body-size (important for metabolic rates and prey selection), trophic position, and feeding habits (*cf.* Chapter 2.2). Correspondingly, to counterbalance for the consequent loss of information, the diet composition and size (in relation to occurrence) of species in each of the families was averaged. Reliable data for microinvertebrates, microphytes, macrophytes and detritus were not available for the Millstream so energy inputs from those sources were all represented as input from the environment, rather then as nodes in the web.

Node names were written in NOUN style throughout the text to indicate clearly the species node to which they refer. When model results were put into context with studies of natural systems, this naming convention seemed to be the most elegant solution to avoid confusion. DACE therefore represents a node with the mean body size and diet composition of dace (*Leuciscus leuciscus*). Fish nodes were characterised by their English name, macroinvertebrate nodes by the Latin names of family or taxa. The food web contains eight macroinvertebrate nodes and 14 fish nodes of which eel (*Anguilla anguilla*) and *E. lucius* were represented in three nodes, respectively, to account for their changing body size and diet composition during ontogeny (Appendix, Table A.3). The starting stock values for fish were mean values of nine electrofishing surveys in the Millstream. The macroinvertebrate starting values were estimated from different surveys as outlined. Energy flow rates were based on ingestion rates for the size of the average individual of that group and

their diet compositions were taken from the literature. In the following section, the application of EcoNet as a modelling tool, and the calculation of the starting stock values, energy flow rates and parametrisation of the model are described.

Calculation of the starting stock values

Fish species For the analysis, only the data for spring, summer and autumn were taken into account, because macroinvertebrate biomass is lower during the winter months and correspond to a period of restricted growth for fish. To calculate the biomass of each species and, subsequently, their energy values, fishes were initially grouped into the following size categories (<5, 5–9.9, 10–19.9, 20–20.9 cm FL, etc), the mean fork length in each size category calculated and then transformed into biomass using calculated or published length-weight relationships (Appendix, Table A.1). Overall biomass in each fish category was obtained by multiplying the mean fish biomass by the total abundance of fish in that category. Finally, the total biomass was converted into energy per gram wet weight values, obtained from Cummins and Wuycheck (1971). The energy values for the size categories were then summed to obtain the starting stock values for each node, which is measured as energy per area [cal m^{-2}].

Macroinvertebrates species To calculate the species biomass per 100 m^2 (i.e. not families), species abundances per family were transformed into dry weight using species mean body length (Tachet et al., 2000) and associated length-weight relationships (Collins, 1992; Benke et al., 1999). The species (or species group) biomass were subsequently converted into wet weight (1 g of wet weight = 0.23 g of dry weight, calculated from measured overall wet weight). Cummins and Wuycheck (1971) provided the conversion factors [cal g^{-1}] to transform these species biomass values into energy values [cal]. Energy values per area of single species were summed according to families to obtain the starting stock values [cal m^{-2}].

Calculation of energy flow rates

The *Flow Rate* characterises how much matter or energy is passed on from one compartment to another per time step. To calculate the flow rate between the compartments an extensive literature research was undertaken.

Fish species Diet of fish was determined from literature, where data on stomach contents analysis were available. The amount of energy passed between the compartments had to be then calculated from these data. Studies undertaken in the Frome catchment were preferred when available (Table 3.1), and prey items (macroinvertebrates) were determined to family level. Presuming that predators encountered and fed on abundant prey more frequently than scarce prey, abundance relationships of macroinvertebrates built the basis to estimate the energy transfer from prey to predator. For some species, this may not be true (selective feeding), but it has been shown for fish that their diet composition tends to reflect seasonal availability of their putative prey items (Mann, 1982). Diet shifts that would occur seasonally due to availability of prey were not accounted for, but mean prey item numbers per season across the years were used to calculate energy flow. Three main methods to determine gut contents in fish were used in the searched literature: number-, occurrence-, and biomass method (Appendix, Table B.1 for advantages and disadvantages of methods). Wherever possible, number of prey items were used to calculate energy flow, as it was the most frequent method used.

Macroinvertebrates species To establish the feeding links of macroinvertebrates, the database of Tachet et al. (2000) was used. This used a fuzzy coding procedure in which the relevant features of a taxon (e.g. diet) were described by the relative distribution of the assigned affinity values (from 0 - no affinity to 5 - high affinity). As there was no detailed information available on diets of predatory macroinvertebrate, predatory macroinvertebrate families were allowed to prey on all other macroinvertebrate nodes. The affinity values for diet composition were converted into percentage values to determine the proportion of energy flow, and the ingestion rate of an

Table 3.1: References and locations for stomach content analysis used for diet determination.

Fish species	Location	Reference
Anguilla anguilla	Tadnoll Brook, Dorset	Mann and Blackburn (1991)
Barbatula barbatula	River Ouzel, Milton Keynes	Hyslop (1982)
	River Endrick, Scotland	Maitland (1965)
Cottus gobio	River Ouzel, Milton Keynes	Hyslop (1982)
	Oberer Seebach, Austria	Adamicka (1991)
Esox lucius	River Frome, Dorset	Mann (1982)
Gobio gobio	River Larraun, Northern Spain	Oscoz et al. (2006)
Leuciscus leuciscus	River Stour (Frome)	Mann (1974)
Phoxinus phoxinus	River Endrick, Scotland	Maitland (1965)
Rutilus rutilus	River Stour and Frome (Average)	Mann (1971)
Salmo salar	River Endrick, Scotland	Maitland (1965)
	Tadnoll Brook, Dorset	Mann et al. (1989)
Salmo trutta	River Endrick, Scotland	Maitland (1965)
	Tadnoll Brook, Dorset	Mann et al. (1989)
	Walla Brook, Dartmoor	Horton (1961)

average macroinvertebrate node was estimated depending on body-size. The diet information for macroinvertebrates consisted of nine categories: microorganisms, detritus ($<$ 1mm), dead plant ($\geq$ 1mm) living microphytes, living macrophytes, dead animal ($\geq$ 1mm), living microinvertebrates, living macroinvertebrates, and vertebrates. Presently, the model consists of macroinvertebrate and fish nodes, so energy input from other sources were represented as environmental inputs.

EcoNet can currently handle 2 different energy flow types, *i*) donor-controlled flow and *ii*) donor-recipient controlled flow.

Donor controlled flow (c): Here, the speed of the energy flow is solely dependent on the storage value (abundance) of the donor compartment; "c" represents the flow coefficient and is proportional to the speed of flow (e.g. energy passed from prey compartment to predator compartment per time unit, i.e. consumption rate). $\Delta E_c = c \cdot A$, where A is the storage value of the prey.

Donor-recipient controlled flow (r): Here, the speed of the energy flow is dependent on the storage values of both compartments. "r" represents the flow coefficient

$\Delta E_r = r \cdot A \cdot B$), where A is the storage value of the prey, and B is the storage value of the predator.

In most food webs, the amount of energy transferred is dependent on both: consumer and resource abundance (Lotka-Volterra type kinetics; Kazanci, 2007). Therefore, the donor-recipient controlled flow was chosen for all predation links between nodes. For constant inputs from the environment and outflows (e.g. respiration, excretion), which are only dependent on one compartment, the donor-controlled flow was used. The following parameters were known to calculate the flow rates:

- The total amount of energy a node received from all its prey items was based on the ingestion rate I calculated from its average body weight.
- The relations, i.e. how much energy is received from a single prey node, was based on diet compositions from the literature.
- The starting stock values (A: starting stock value prey; B: starting stock value predator) was based on measured mean abundances.
- Outflows were based on literature values of energy assimilation efficiency.

The metabolic rate R scales with body size, which means that small organisms have a higher metabolic rate per gram than large organisms. For the calculations, the ingestion rate was used, which, for poikilotherms, is ≈ 3.3 times standard metabolic rate (Peters, 1983). Ingestion rates for all nodes were calculated as: $I = 0.779W^{0.82}$, with W: body weight [kg] (ingestion rate for carnivorous poikilotherms, Peters, 1983) and normalised to area [m^2].

The donor-recipient controlled flow calculates the change of energy (ΔE) between two nodes A and B as:

$\Delta E_{AB} = r_{AB} \cdot A \cdot B$, with r_{AB}: specific flow rate between prey A and predator B; A and B: starting stock values of prey and predator. ΔE_{AB} corresponds to a fraction of the predator's ingestion rate I_B [cal m^{-2} d^{-1}] as obtained from the diet compositions.

$\Delta E_{AB} = x_i \cdot I_B$, with $0 < x_i < 1$ and $\sum x_i = 1$.

The energy flow rate r_{AB} is therefore:

$$\begin{aligned} r_{AB} \cdot A \cdot B &= x_i \cdot I_B \\ r_{AB} &= \frac{x_i \cdot I_B}{A \cdot B} \end{aligned}$$

Energy inputs from sources that are not represented as nodes entered the food web from the environment and outflows that represent energy loss (except predation) leave the food web into the environment. The environment can be interpreted as an energy pool of infinite size, in contrast to nodes that change their stock values dependent on in- and outflows. Energy inputs were a fraction of the ingestion rate, if the organisms represented in that node fed on other nodes:

$c_{env} = x_i \cdot \Delta E$, with $0 < x < 1$ and $\sum x_i = 1$, c_{env}: flow rate from the environment.

If node A receives all its energy from sources not represented as nodes, then $c_{env} = I_A$, with I_A: ingestion rate for node A.

Not all energy that is transferred from one node to the next remains available. Approximately 70–95% of the energy intake is lost to the environment (e.g. respiration, excretion) and not accumulated as biomass (e.g. growth, reproduction). The outflow rates for all nodes were based on the assumption that 90% of the ingested energy is lost and were calculated as:

$c_{outflow} = \frac{0.9 \cdot I_A}{A}$, with A: starting stock value of a node, I_A: Ingestion rate of node A.

Model parametrisation

The model was run with the calculated starting stock values and flow rates, and the stock values in steady state were recorded. With the adaptive time step method of EcoNet, the parameters *max time steps* and *sensitivity* could be adjusted to alter model performance. The influence of changing these parameters on the model output

was tested. While changes of the *sensitivity* parameter did not have an effect on the model output, it was important to choose the *max time step* parameter sufficiently large for the model to reach steady state.

To achieve a final stable state that resembled the original food web model, additional energy inputs were given at different levels, and the final stock values were recorded. Based on those findings, values were chosen to create the Baseline Model, which was manipulated in the following chapters. The additional energy input came from the environment and could also be interpreted as immigration, and not only energy input from compartments that were not represented as nodes, such as primary producers or detritus.

Trials were run in which the additional energy input was increased by 10, 20, 30, 40, 50, 100% of the ingestion rate. This additional input is given

1. Only to macroinvertebrate nodes.
2. Only to fish nodes.
3. To both nodes.

Statistical methods

The final stock values for each run were recorded and the distance of the resulting communities to the starting stock values was measured using the Bray-Curtis dissimilarity measure. The Bray-Curtis coefficient (S_{jk}) is a robust measure of the similarity between two communities, and it is the recommended coefficient to analyse biological data on community structure (Faith et al., 1987). It is calculated as:

$$S_{jk} = 100\left\{1 - \frac{\sum_{i=1}^{p}|y_{ij}-y_{ik}|}{\sum_{i=1}^{p}(y_{ij}+y_{ik})}\right\}$$

where y_{ij} is the abundance of the ith species in the jth sample, and y_{ik} is the abundance of the ith species in the kth sample. The coefficient equals 100 when two

communities are identical and it equals zero when the two compared communities are completely different. The Bray-Curtis dissimilarity is thus calculated as $100 - S_{jk}$. The resulting matrix of coefficients was analysed using Kruskal's non-metric Multi Dimensional Scaling (MDS) ordination (Kruskal, 1964a,b). It is assumed for the MDS that there should be a rank-order relationship of the similarity between the communities, as calculated by a similarity measure, and the distance in ordination space (Fasham, 1977). Similar communities are mapped close together, whereas dissimilar ones are mapped further away and so the distance between two points matches the dissimilarity value. The method was chosen because MDS has been demonstrated as a robust unconstrained ordination method in ecology (Field et al., 1982; Kenkel and Orloci, 1986; Minchin, 1987). Unconstrained methods are useful to display broad patterns in a data cloud if the response variable, in this case species abundance, is not linked to a predictor variable, such as environmental variables (Anderson and Willis, 2003). As high dimensional data is mapped on fewer dimensions, compromises are made in terms of accuracy in desplaying the distances between the data points. Stress is a measure of badness of fit and needs to be considered when interpreting the data (Kruskal and Wish, 1978). High stress indicates that distances between data points are distorted. Generally, the amount of acceptable stress will vary from application to application (Quist and Yona, 2004), but stress below 0.1 (10%) are considered excellent, whereas stress above 0.15 (15%) is unacceptable (Kruskal and Wish, 1978). In the case of high stress, larger distances reflect the data better than smaller ones, which has to be taken into account when the data is interpreted. So even with high stress, a global pattern can still be grasped.

3.3 Results

The network graph produced by EcoNet (Figure 3.4) shows the direction of the energy flows and the position of the nodes correspond to their trophic position. Oligochaeta and Ephemeroptera received all their energy from the environment, whereas all other macroinvertebrates were predatory to some extent.

When the model was run with the calculated values, the stock values of thirteen nodes declined to zero. The consequent rise in energy inputs had different effects on network behaviour at different levels. Increasing energy input at the macroinvertebrate level caused the stock values to fluctuate before the model relaxed into a stable state. The additional energy did not propagate to higher levels of the food web and extinction rates remained high (Table 3.2). Trout, Gudgeon, Pike2, Pike3, and Eel_1 were the only fish nodes still present at steady state. Extinctions decreased to zero when additional energy input was given into only fish nodes. In those cases, the model relaxed faster into steady state ($\approx$ 1000 time steps compared to 10,000 when additional energy was only given to macroinvertebrate nodes). Pike2 and Pike3 abundance increased by 500%, whereas most other nodes showed a decline at the highest additional input rate. Similar model outputs were observed when additional input was given into all nodes at the same time. The main difference was that Gammaridae and Mollusca doubled in abundance. In all cases Bullhead showed a large decline. MDS ordination (Figure 3.3) supported that energy inputs into only macroinvertebrate nodes did not move those communities closer to the community with the initial abundances, whereas additional input into all nodes and only fish nodes did. Inputs around 50% into only fish nodes or all nodes yielded communities closest to the starting values. However, direct comparison of the final stock values with the initial values showed that the similarity was not sufficient to proceed with further manipulation of the model. The additional energy input was altered to achieve a model that resembled the initial values better. Most of the final values that were used for further manipulation of the model (Appendix, Table A.4) lay between 10% and 30% of the ingestion rate with a few

exceptions. Relatively, macroinvertebrate nodes with low abundance received much higher additional energy inputs (Coleoptera, Plecoptera, Ephemeroptera, Trichoptera) than the more abundant nodes, such as Gammaridae, Mollusca and Oligochaeta. Bullhead, as the only fish node, also received a high environmental energy input relative to its calculated ingestion rate.

Table 3.2: Number of extinctions for communities after additional energy inputs were received by: firstly, only macroinvertebrate nodes; secondly, only fish nodes; and thirdly, all nodes. In comparison, without additional energy inputs thirteen extinctions occurred and no extinctions occurred in the chosen Baseline Model.

Energy input raised by	Macroinvertebrate nodes	Fish nodes	All nodes
10%	10	1	1
20%	10	1	1
30%	10	1	1
40%	11	1	1
50%	10	1	1
100%	10	1	1

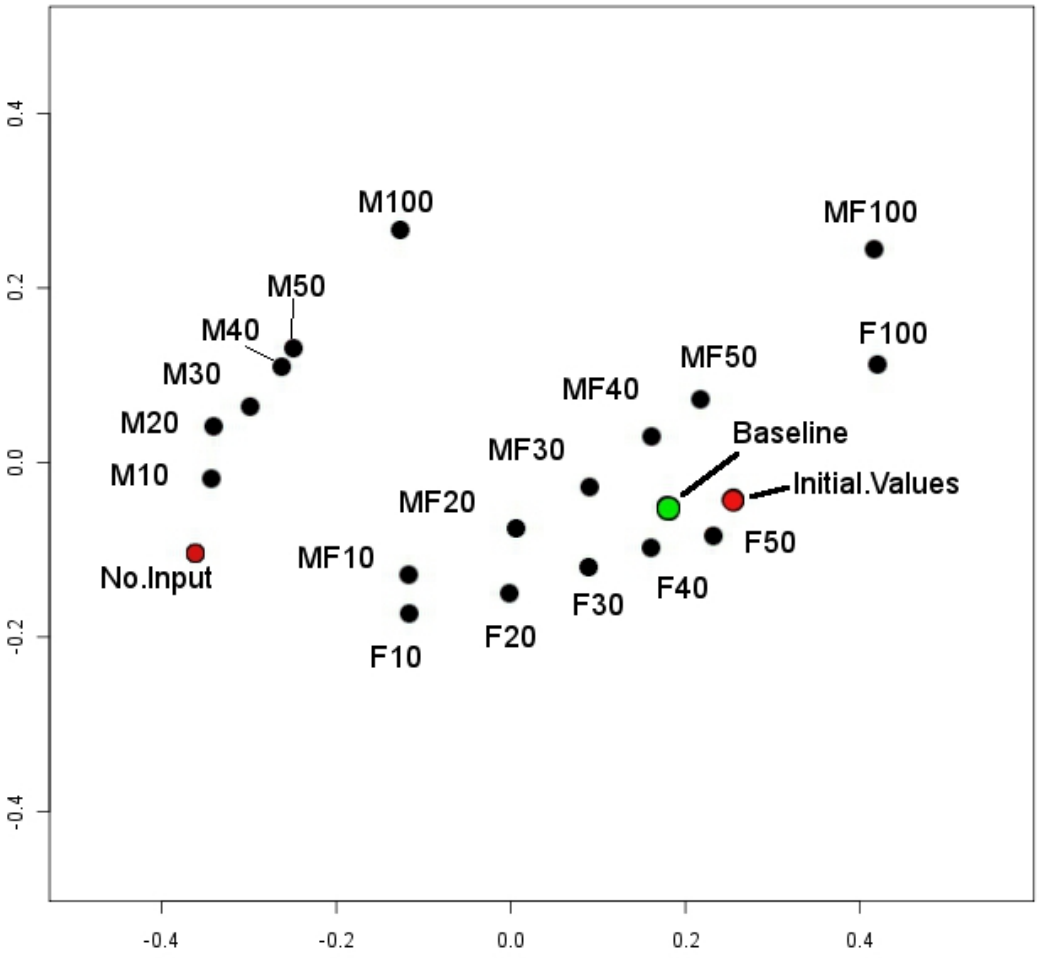


Figure 3.3: MDS for resulting communities after additional energy input at different levels. **M**: only macroinvertebrate nodes, **F**: only fish nodes, **MF**: macroinvertebrates and fish nodes receive additional energy. Stress: 4.14%.

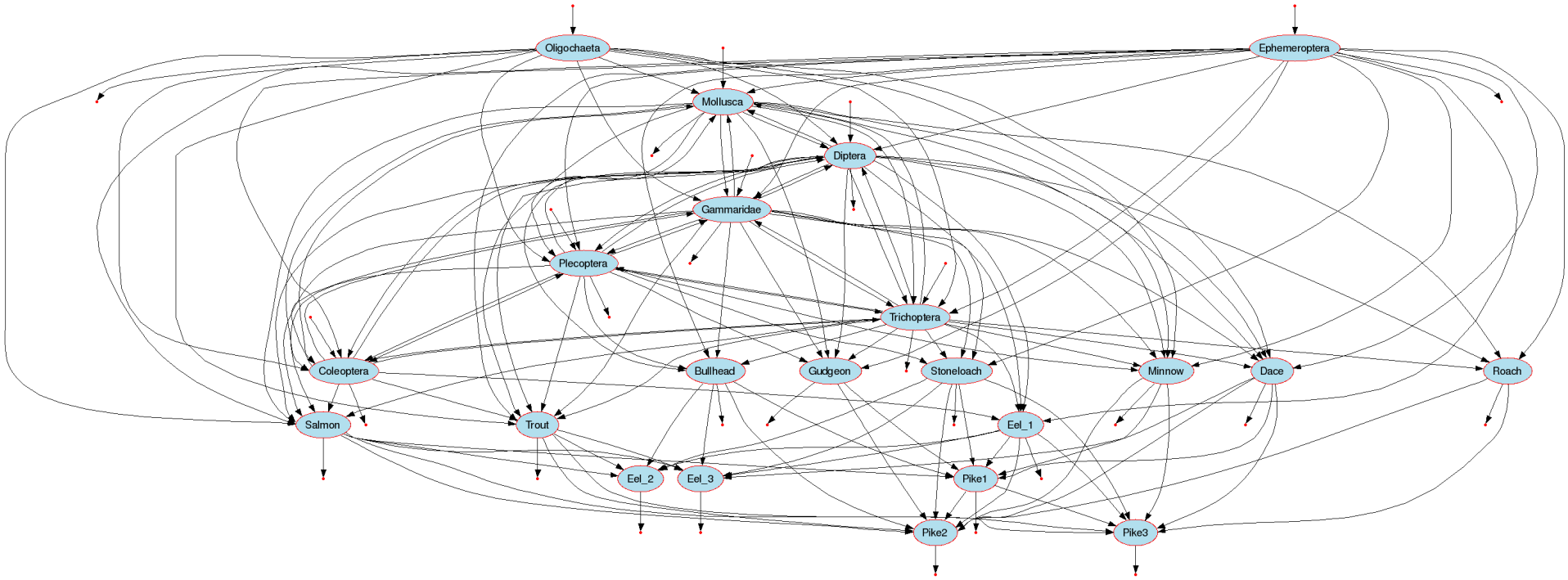


Figure 3.4: Network graph for the Baseline Model. The lowest trophic level can be found at the top of the graph, flows between the compartments are marked with an arrow and a "*" marks the environment.

3.4 Discussion

The dynamic model reached a final steady state with similar abundances as the initial starting values with additional environmental energy inputs. Without these energy inputs, extinctions were frequent and the model would not have been suitable for further manipulation. The additional energy input from the environment was justifiable since the ingestion rate used for the calculation of the energy flow rates were approximate values and, in addition, these inputs can be interpreted as immigration. The stabilising effect of higher energy input has also been found for simple, three compartment energy flow models (O'Neill, 1976) where the return time after a disturbance decreases as the rate of energy flow into the system *via* the autotroph compartment increases. Here, additional energy input into the lower levels (macroinvertebrate nodes) alone did not move the resulting communities closer to the initial starting values, and the number of extinctions remained high. This finding suggested that the additional energy did not travel to higher levels of the food web sufficiently to avoid the observed extinctions. A possible explanation could be the architecture of the food web. By aggregating macroinvertebrate into trophic species, the resolution at this level of the food web was lower than for the fish nodes. The aggregation of macroinvertebrate species was taxonomic and although it would have been desirable to represent these species in trophic guilds, the available diet compositions for fish and macroinvertebrates did not allow this. Instead, the mean diet composition and body-size of the species in a family were used to establish the energy flows to other nodes. In the case of predatory macroinvertebrate families, all the predatory invertebrate nodes preyed on each other, introducing feedback loops. Those loops might be the reason for additional energy loss, since only 10% of the ingested energy is used for growth and available to the next predator. Environmental energy input into fish nodes solved the problem and could substitute the lost energy. If energy does not travel up the food web sufficiently because of aggregation (less diversity, changed hierarchy), then the interpretation of changes in abundance of macroinvertebrate nodes after manipulation of the Baseline Model is unlikely to correspond to natural dynamics of the natural food web. Possible bottom-up ef-

fects could be attenuated. However, bottom up effects could be the reason for the strong increase in GAMMARUS and MOLLUSCA abundance when additional energy was given to macroinvertebrate and fish nodes compared to the food webs, where additional energy was only given to fish nodes. In the energy input experiments for only fish, not only fish nodes, but the entire food web stabilised dramatically. When additional energy was given to all nodes, top-down effects were possibly attenuated, resulting in higher macroinvertebrate abundances. BULLHEAD declined in all cases and required a relatively large additional energy input to produce the Baseline Model. Compared to e.g. DACE, BULLHEAD has a less specialised diet and hence should not be as dependent on the abundance of single nodes. Therefore, it is likely that predator pressure on BULLHEAD let to the decline in its abundance.

Aggregation of species has been found to affect system indices of ecological network analysis and change the global structure of the food web (Ulanowicz and AbarcaArenas, 1997; Abarca-Arenas and Ulanowicz, 2002; Baird et al., 2009), particularly when aggregations are made on the lower levels of the network (Johnson et al., 2009b). Aggregation of detritus pools can also have serious consequences on network results (Allesina et al., 2005). These findings have consequences for the comparison of ecosystems with different aggregations, but comparison of networks constructed with the same constraints can still achieve useful predictions (Allesina et al., 2005). Consequently, aggregated macroinvertebrate nodes should primarily be viewed as food sources for fish nodes in the present model and predictions regarding the change in abundance of those nodes are very general.

Increased biodiversity can lead to greater ecological stability (diversity-stability hypothesis; Elton, 1958). Biodiversity is not the only factor responsible for stability in ecosystems, as the pattern in which nodes are connected (May, 1972) and seasonal dynamics can be important (Chapter 2). The aggregation of macroinvertebrates into families was a simplification that disregarded the heterogeneity of a natural river food web caused by seasonal dynamics and species diversity. Species and species aggregations were represented as 'super organisms' that interacted only through predation links and were evenly distributed over space. Consequently, biodiversity and het-

erogeneity effects on stability that are observed in natural systems (Chapter 2) may not translate in the present food web model.

The literature that was used to determine the diet compositions spans several decades of climate warming (Table 3.1). Fish diet can reflect macroinvertebrate community composition to a certain extent, as more abundant prey is encountered more often, although selective feeding has been shown as well (Mann, 1982). Potentially, macroinvertebrate community composition and consequently fish diets have already changed over the decades. Unfortunately, comparison of potential long term changes in macroinvertebrate community composition from the diet compositions is not possible, because diets were taken in different locations, and the influence of location is likely to be greater than the influence of climate change.

The natural chalk stream environment is highly heterogeneous, with smaller subsystems connected by larger, more mobile species (Woodward et al., 2005a). Macroinvertebrate communities differ in composition dependent on the substrate they live on (e.g. gravel and *Ranunculus* patches). Stabilising effects that might be promoted by heterogeneous environments and sub-communities are not captured intrinsically in the model. Additionally, areas that are less accessible for predators, such as small ditches or shallow riffles, might serve as refugia. Food web dynamics and growth rates would be different in such an environment and individuals could migrate and repopulate other areas from there. Despite the findings that species aggregation can alter food web properties, the aggregation of nodes is general practise, especially on the lower levels of food webs (Fath, 2004; Baird et al., 2009). Information on energetics and diets are, in general, not as available for the base of the food web as was the case in the present study (Baird et al., 2009). Although some of the values for the additional energy are very high relative to the calculated ingestion rate, this is not necessarily a problem when the model is manipulated to assess the impact of disturbances, since the change to the Baseline Model will be assessed. Nonetheless, these points have to be kept in mind when interpreting the results.

Chapter 4

Impact of species removals on community composition

4.1 Introduction

The resilience of aquatic ecosystems to disturbances is of great concern in the background of the current rate of environmental change. Only healthy ecosystems deliver important goods and services to society (e.g. drinking water, fisheries, and recreation). A healthy ecosystem "has the ability to maintain its structure and function over time in the face of external stress" (Costanza et al., 1997). The current exceptionally high extinction rates, which can be largely attributed to human activity (Lawton and May, 1996), can threaten ecosystem function and therefore the supply of ecosystem services (Chapin et al., 2000; Hooper et al., 2005; Hector and Bagchi, 2007; Gamfeldt et al., 2008; Woodward, 2009). Ecosystem function has been linked to community structure, but how single species or communities contribute to ecosystem services remains poorly understood (Larsen et al., 2005).

The resilience to perturbations and the stability of an ecosystem can be investigated by deleting species from model food webs and investigating the consequences on community composition (Pimm, 1980). Species deletion corresponds to a large and persistent perturbation after which the remaining species reach a new equilibrium

(Pimm, 1982), moving from one 'domain of attraction' to another (Amoros et al., 1987). In addition, the loss of one species can cause subsequent cascading extinctions, resulting in further loss of biodiversity (*cf.* Chapter 2). Complex communities (i.e. higher connectance) seem to be more robust to species loss than simple communities, if the lost species is not a top predator (Eklof and Ebenman, 2006). Also, omnivory and triangular food web structure (less top species than intermediate and basal species) can reduce secondary extinctions after the loss of intermediate species (Petchey et al., 2004). In these cases, predator impacts after the loss of a prey species could be diluted as higher connectance, omnivory and triangular food web structure all ensure that more links to prey species remain than in less complex communities or in ones with rectangular food web structure (same amount of species on all trophic levels). Top predators can mediate competitive interactions of their resources, so the removal of a top predator can cause dominant prey species to out-compete less dominant ones, resulting in secondary extinctions (Paine, 1969b). Even when the loss of one species is not followed by secondary extinctions, it can have major effects on the abundance of the remaining species, and, accordingly, change community structure (Power, 1990).

Species that significantly shape the structure of an ecosystem are called keystone species and have been shown to elicit a cascade of events when removed, influencing not only the abundance of species directly connected to them (e.g. *via* energy, material flow or behavioural interactions), but also indirectly. The term keystone species is used very broadly in the literature (Lamont, 1992; Bond, 1993; Mills et al., 1993; Paine, 1995; Power and Mills, 1995; Folke et al., 1996; Power and Tilman, 1996; Hurlbert, 1997; Piraino et al., 2002; Davic, 2003). Originally defined as "a species of high trophic status whose activities exert a disproportionate influence on the pattern of species diversity in a community" (Paine, 1969b), the term 'keystone' is also applied to species that have a large effect on any aspect of ecosystem function, e.g. keystone-engineers, -prey, -pollinator. Since keystone species have such a large influence on ecosystem structure, their identification can give valuable recommendations for ecosystem management and conservation (Jordan, 2009).

Within the model framework (*cf.* Chapter 3), the removal of a keystone species should be identified by a significant and irreversible system shift to a new local stable state. In contrast, redundant species would not elicit such a shift when removed from the system. As the proposed model simulates energy flows, system shifts that are caused by interactions, such as habitat modification or behavioural interactions, cannot be investigated in the present study.

Assessing a system shift is not trivial. The traditional measure used to identify a trophic cascade is a change in productivity measured as change in plant biomass (Polis et al., 2000). However, impacts on detritus processing rates have also been used to quantify such keystone effects (Woodward et al., 2008). These measures are not applicable in the present study, because the dynamic food web model does not quantify primary producers and detritus. Here, the applied measure to identify a system shift is characterised by a significant change in community composition, when compared to the initial food web structure. Populations naturally fluctuate over time, while the ecosystem maintains an equal set of processes (Holling, 1973, *cf.* Chapter 2). The challenge is to define a set of states (community compositions) that reflects this natural variability and can be used as reference state or reference dynamic. In the dynamic food web model, the starting stock values for nodes are mean values from measurements over a three year period (*cf.* Chapter 3). These measured abundances reflect the natural fluctuations in community compositions specific to the Millstream, while the ecosystem is considered undisturbed, and thus can be used to define the reference dynamic.

The resilience of ecosystems has been linked to biodiversity (Loreau and Behera, 1999; Elmqvist et al., 2003). A reduction of biodiversity can make an ecosystem more vulnerable to external perturbations (Woodiwiss, 1964; Dangles and Guerold, 1999; Stachowicz et al., 1999; Chapin et al., 2000; Knowlton, 2001; Scheffer et al., 2001; Folke et al., 2004) and reduce processing rates (e.g. leaf litter breakdown rates) with consequences on ecosystem function (Hughes, 1994; Walker et al., 1999; Jonsson et al., 2002). Paine (1969b) suggested a link between the removal of a keystone species and a subsequent decline in biodiversity, because competitive interactions

are no longer mediated by a predator. Consequently, as processing rates cannot be determined directly from the dynamic food web model, a decrease in biodiversity after species removal appears to be a useful additional measure for the identification of keystone species and for ecosystem resilience. One aspect of biodiversity loss is a reduction in species richness (Magurran, 2004). When the loss of a species is followed by cascading (secondary) extinctions, major changes in ecosystem properties (e.g. changes in biomass on different trophic levels) can be observed (Thebault et al., 2007).

Lately, an emphasis has been put on the importance to link ecosystem services and changes in biodiversity (Thebault et al., 2007). One typical freshwater ecosystem service concerns nutrient cycling and retention. Since the classic measure for productivity (primary production) is not available in the dynamic food web model, changes in secondary production can be used as a measure for ecosystem function (Duffy, 2002). In particular, decreases in fish production could be of high economic interest (Holmlund and Hammer, 1999). If the loss of a keystone species is followed by a decrease in biodiversity, then this could be reflected in a decrease of secondary production (Schlapfer and Schmid, 1999), although it has also been found that competition can dampen the effect, as the biomass of the remaining, dominant species increases, while biodiversity decreases (King and Pimm, 1983; Pimm, 1984).

Aims and objectives

The aim of this chapter is to identify the presence of keystone species in the Millstream through manipulations of the dynamic food web by species removals and measuring the extent of change in measures of species diversity, community composition and secondary production.

4.2 Material and Methods

4.2.1 Manipulation of the Baseline Model - single species removal

As in the previous chapter, the food web nodes are characterised by NOUN style (Table A.3). From the Baseline Model developed in Chapter 3 (Figure 3.4), each node was removed in turn, with the exception of PIKE and EEL, where three nodes were removed (PIKE1, 2, and 3; EEL_1, 2 and 3). When a prey node was removed, the predator covered its consumption (defined by the ingestion rate) proportionally through higher predation rates on the remaining prey that form part of its diet. The models were run for 5000 time-steps with a sensitivity value of 0.1 (*cf.* Chapter 3). The final stock values for each species were recorded, and the resulting communities were named after the node that has been removed. For example, the community named "R_Trout" is the resulting community after TROUT removal. The Shannon index was used to assess species diversity and compared to the Baseline Model to assess changes. The amount of secondary extinctions was also recorded. Kruskal's Non-metric Multidimensional scaling (MDS) analysis was used to identify the similarity of resulting communities (*cf.* Chapter 3). A system shift was identified if the resulting community after a removal was more dissimilar than the natural variability of the system, which was defined by the measured fish abundances from the Millstream. Finally, changes in secondary production were compared to changes in biodiversity.

4.2.2 Diversity measure and secondary extinctions

To assess the change in diversity after species removals, the Shannon-Wiener measure of diversity (H') was calculated and then converted into effective number of species (true diversity). This conversion is advantageous because (*i*) the measure is intuitive, since it reflects the number of equally common species in the community; and (*ii*)

true diversity can be calculated for other diversity indices, such as the Simpson's index, so the diversity of communities can be compared even when different diversity indices were used (Jost, 2006).

The Shannon index is calculated as:

$$H' = \sum_{j=1}^{S} p_j \cdot \ln p_j,$$

where p_j is the proportion of species j (abundance of species j divided by the total abundance of species) and S is the total number of species in the assemblage. H' increases with greater number of species and greater evenness, and the maximum value is achieved when all species are equally abundant ($H'_{max} = \ln S$). Values fall usually between 1.5 and 3.5 (Margalef, 1972). The Shannon index was calculated with the abundances defined in cal m^{-2}, and was then converted into effective number of species ($\exp(H')$). The following example illustrates the advantage of comparing effective number of species. Consider a community with a Shannon index of $H' = 3$, and a second community with $H' = 2.5$. It is not obvious from the difference of the Shannon index how distinct the diversities of these communities are. However, when the true diversity is calculated, ($\exp(3) = 20$; $\exp(2.5) = 12$) it becomes obvious that the first community is almost twice as diverse as the latter.

When a node is removed from the model, diversity is expected to decrease. This expected decrease was calculated for each removal community by calculating the effective number of species for the final stock values of the Baseline Model omitting the removed node. δ_{div} is the difference of the expected diversity $\exp(H'_{exp})$ and the diversity calculated from the model output for each removal community $\exp(H'_{Model})$.

$$\delta_{div} = \exp(H'_{Model}) - \exp(H'_{exp}).$$

δ_{div} serves as a measure for impacts on diversity that cannot be attributed to the species abundance, but must be due to other specifics of the species nodes, such as diet composition and interaction strength. There are three possible outcomes:

1. $\delta_{div} = 0$, the community is less diverse compared to the Baseline Model because one species was removed. However, there are no knock on effects on the

remaining community.

2. $\delta_{div} > 0$, the community is more diverse than expected. There are positive knock on effects on the community after species removal.

3. $\delta_{div} < 0$, the community is less diverse than expected. There are negative knock on effects on the community after species removal.

Additionally, the number of secondary extinctions was recorded.

4.2.3 Comparison of the communities

The resulting communities were compared using the Bray-Curtis dissimilarity measure (see Chapter 3.2.3). The similarity matrix was calculated omitting the terms that include the removed species, so only differences between the remaining nodes were detectable, and not the difference caused by setting one stock value to zero. The resulting coefficients were analysed using non-metric MDS ordination. In a second step, the results of the MDS are put in relation to the natural variability of the ecosystem. Recorded abundance values from the Millstream for fishes (9 measurements over three years) were compared to the results from the removals. In some of these measurements, not all fish species that are present in the Baseline Model could be recorded and were assumed to be naturally absent. Fish abundances alone were compared in this step, since no corresponding macroinvertebrate abundances were available.

To assess changes in secondary production, the final stock values of all nodes were summed for each community ($E_{spX} = \sum y_i$, with E_{spX}: secondary production of community X; y_i: final stock value of node i) and compared to the secondary production of the Baseline Model. If the removed species had no further effects on network dynamic, then the change in secondary production would be expected to be the difference between the secondary production of the Baseline Model and the starting value of the removed species.

$$\Delta Energy_{expected} = Secondary\,production_{Baseline} - Starting\,Value_{removed\,species}$$

4.3 Results

After 5000 time-steps, the stock values of all models did not change further, and the energy transfer between the compartments was fixed. Therefore, it was assumed that all resulting communities had reached steady state.

4.3.1 Change in biodiversity secondary extinctions

The largest decline in species diversity occurred after Dace removal, followed by Ephemeroptera, Trichoptera, Bullhead and Roach removal (Table 4.1). Dace removal equivalented to $\approx 8\%$ decline in true diversity, while the latter nodes caused a decline around 5%, when compared to the expected diversity. Some removals caused an increase in diversity relative to the expected diversity (Diptera, Pike, and Eel; $\approx 5\%$ increase). In direct comparison to the Baseline Model ($\exp(H') = 12,7$), species diversity declined by $\approx 15\%$ after Dace removal and $\approx 10\%$ after Ephemeroptera, Trichoptera, Bullhead and Roach removal, whereas Diptera removal elicited no change, and Eel and Pike removals were less diverse ($\approx 9\%$).

None of the removals were followed by a complete secondary extinction (stock value reaches zero). However, when extinction was defined as a decrease in abundance of more than 95%, secondary extinction occurred twice for the same species. After Ephemeroptera and Trichoptera removal, Roach abundance declined to 4% of the Baseline Model abundance.

4.3.2 Comparison of the communities: MDS

In a MDS graph, communities that are similar are closer together and those that dissimilar are further apart (Figure 4.1). Most resulting communities were close to the Baseline Model. The communities that showed the largest decline in biodiversity

Table 4.1: Differences of the expected diversity calculated from the model output ($\exp(H')$) and the expected diversity. The expected diversity is calculated from the values of the Baseline model omitting the value of the removed species node. For $\delta_{div} = 0$: no knock on effect after node removal; for $\delta_{div} > 0$: positive knock on effect; for $\delta_{div} < 0$: negative knock on effect.

Removed node	Expected diversity	Model diversity	Difference	δ_{div}
Dace	11.8	10.9	-0.9	
Ephemeroptera	12.6	11.9	-0.6	
Trichoptera	12.4	11.8	-0.6	
Bullhead	12.6	11.9	-0.6	$\delta_{div} < 0$
Roach	11.7	11.2	-0.5	
Gammaridae	12.9	12.7	-0.3	
Gudgeon	12.2	11.9	-0.2	
Minnow	11.7	11.6	-0.1	
Trout	11.7	11.7	0.0	
Salmon	11.7	11.7	0.0	
Plecoptera	12.7	12.7	0.0	$\delta_{div} = 0$
Coleoptera	12.7	12.7	0.0	
Oligochaeta	11.9	11.9	0.0	
Mollusca	11.8	11.9	0.1	
Stoneloach	11.9	12.1	0.1	
Diptera	12.2	12.7	0.5	$\delta_{div} > 0$
Pike	10.9	11.5	0.6	
Eel	10.6	11.2	0.7	
Baseline Model		12.7		

(Removal of Dace, Ephemeroptera, Trichoptera, Bullhead) are also found further away from the Baseline model. Communities after Pike and Eel removals were the the most dissimilar to the Baseline Model, and caused the largest positive change in biodiversity. Assessment of the significance of a particular species removal on community structure was difficult since there is no obvious threshold (distance to the Baseline Model) that indicates a system shift. As such removals were compared to seasonal abundance data of fish species at the study site (Figure 4.2), which suggests that the natural variability in community composition was greater than the changes caused by species removals. Not all species were present at all sampling occasions, e.g. roach was not present in autumn 2004, spring 2004 and 2005. Those three natural communities and the community after roach removal were not found in similar locations (Figure 4.2), which suggests that the absence of a species does

not necessarily have a similar impact on the abundances of the remaining species.

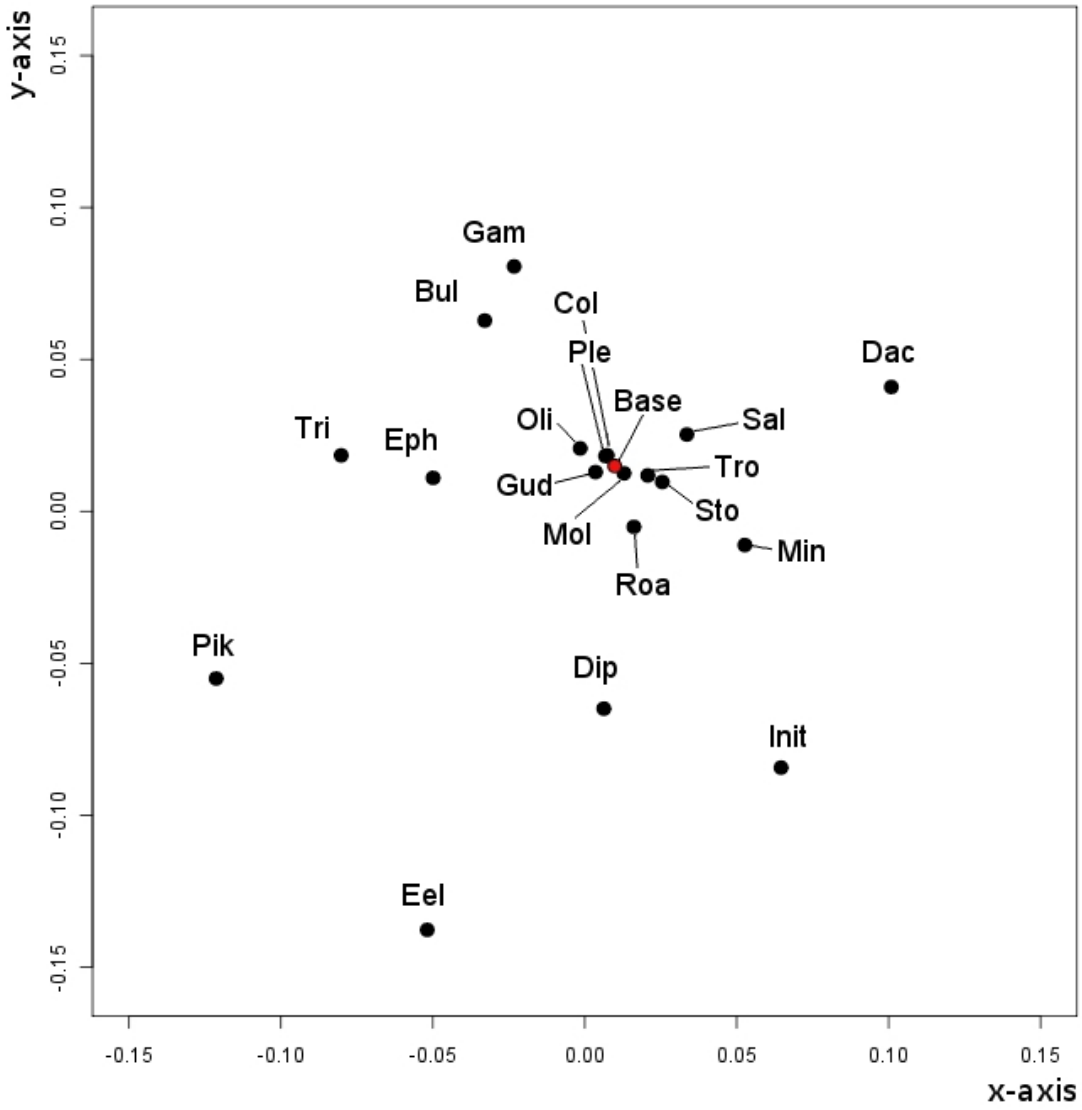


Figure 4.1: MDS ordination for the removal communities. The resulting communities (circles) are labelled with the code for the species that was removed. (**Base:** Baseline Model, **Init**: Initial starting stock values for all model runs; Stress: 14.47%)

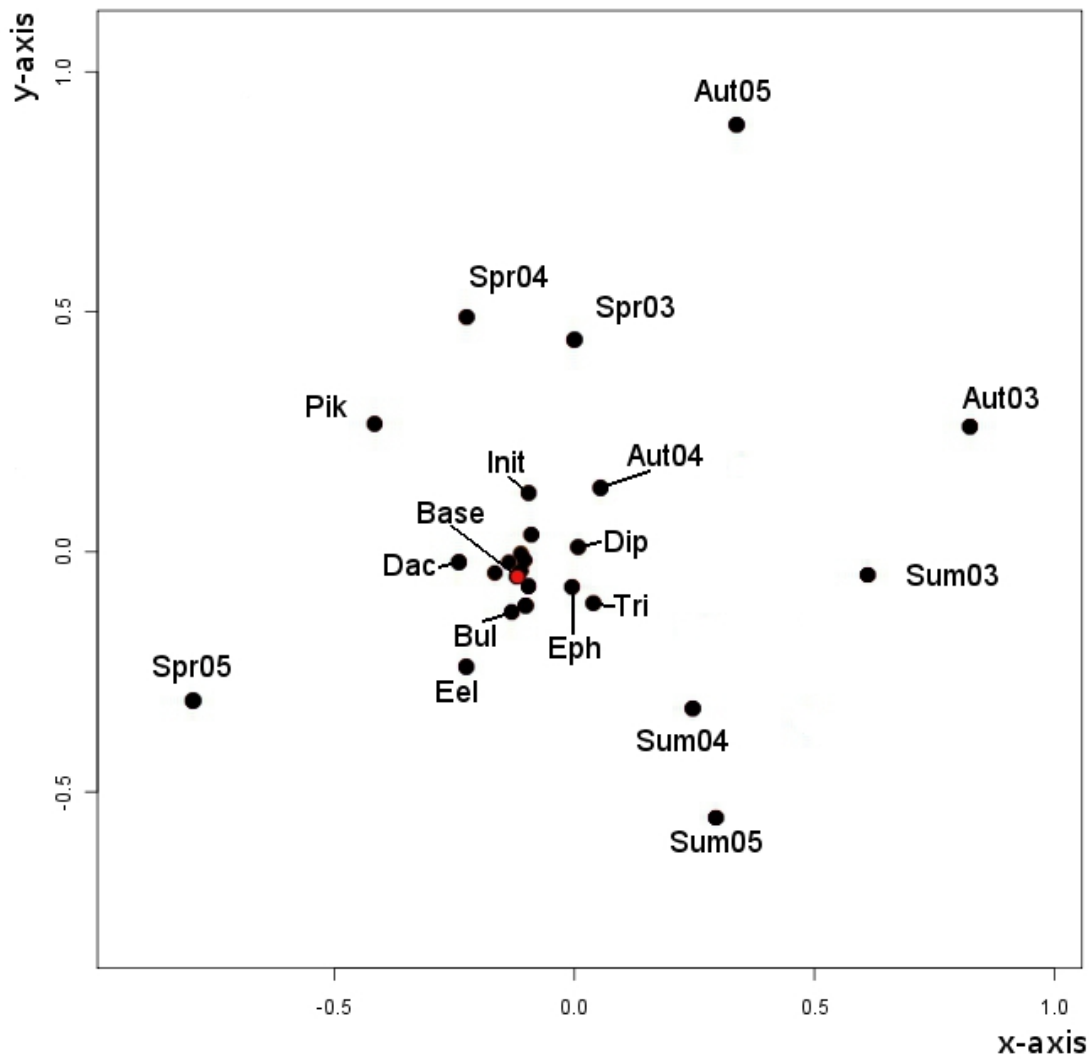


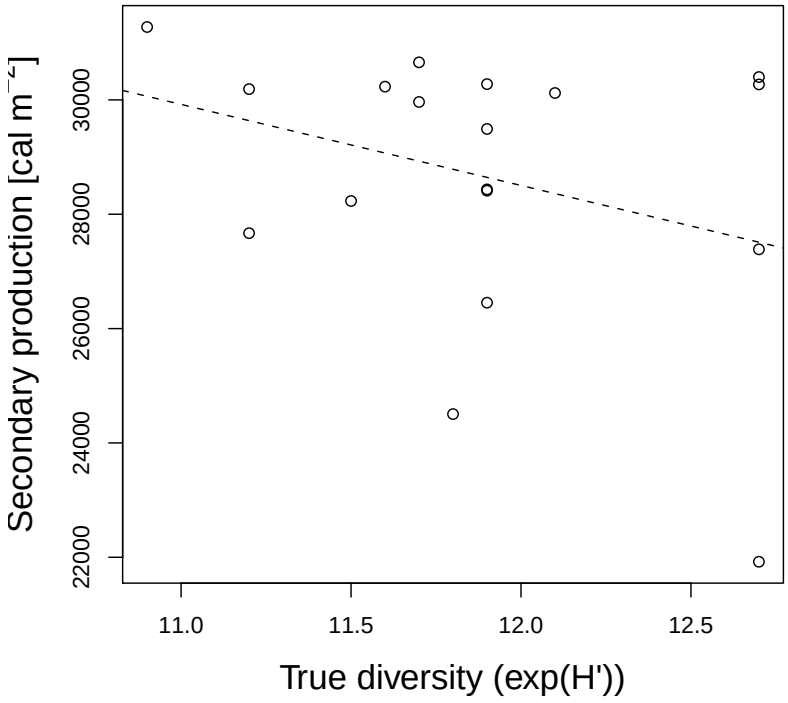
Figure 4.2: MDS ordination for removal and measured communities. The removal communities (see Figure 4.1) are displayed in relation to the measured communities (Spring, Summer, and Autumn 03-05). Only the abundance values of fish nodes where used for the analysis. The abbreviations are the same as in Figure 4.1. Stress: 12.99%.

4.3.3 Change in secondary production

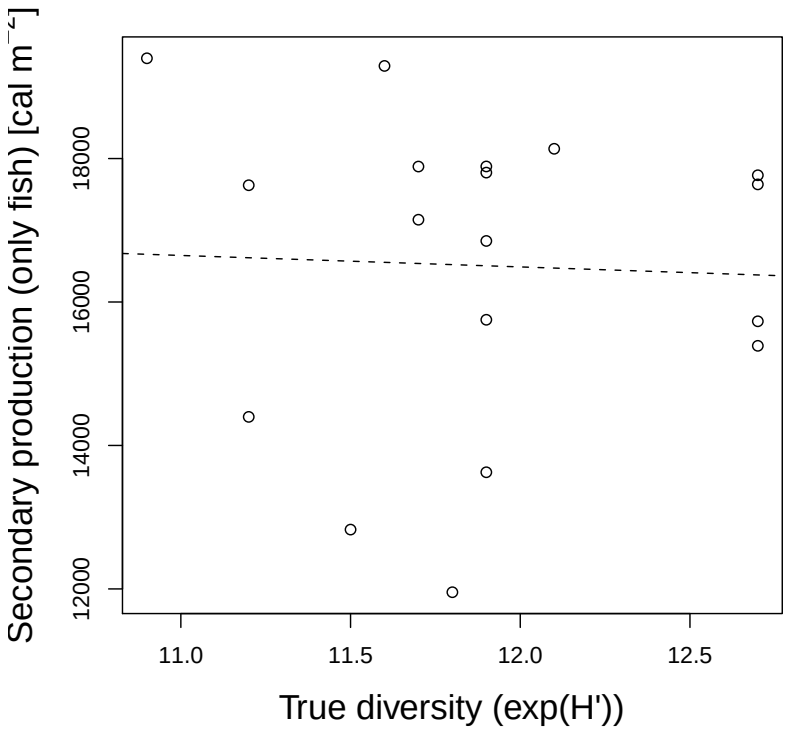
In general, secondary production was lower than expected when macroinvertebrate nodes were removed and higher when fish nodes were removed (Table 4.2). The largest loss of energy from the system was observed after removal of main food sources for fish: Trichoptera, Ephemeroptera, Gammaridae and Diptera. These results suggested that energy was not entering the food web sufficiently when those nodes were removed. Dace, Salmon, Pike and Eel removal caused a larger increase in secondary production than would be expected. Those removals also caused the largest shifts according to the MDS analysis and the largest change in diversity. The change in secondary production was not correlated to the starting stock values of the removed species ($r^2 < 0.1$) and no correlation was found between secondary production and true diversity (Figure 4.3a, $r^2 = 0.1$). There was also no correlation found when secondary production of fish alone were compared to true diversity (Figure 4.3b, $r^2 < 0.1$).

Table 4.2: Difference between observed and expected total energy of the communities after the removal of a species.

Removed node	Difference between observed and expected total energy
Trichoptera	-5851
Ephemeroptera	-4028
Gammaridae	-2832
Diptera	-2578
Oligochaeta	-1026
Plecoptera	-296
Stoneloach	-250
Coleoptera	-160
Roach	13
Gudgeon	38
Mollusca	72
Trout	84
Bullhead	804
Minnow	1285
Eel	1923
Pike	3129
Salmon	5070
Dace	5490



(a)



(b)

Figure 4.3: Correlation of secondary production and biodiversity. (a) There is no correlation between the absolute secondary production and true diversity ($r^2 < 0.1$); and (b), no correlation between secondary production of fish nodes alone and true diversity ($r^2 < 0.1$). The dashed line represents a best fit line in both figures.

4.4 Discussion

Complex communities are said to be more resilient to species loss than simple ones (Naeem and Li, 1997; Eklof and Ebenman, 2006), and this postulate is supported by the results of the present study, which modelled a complex community. Although some species removals had a considerable impact on community structure, none of the removals caused a shift that was considered ecologically significant. All model systems remained within the range of observed variability in species abundances in the study area. For measuring ecosystem resilience, Holling (1973) proposed that a trajectory of the cyclic behaviour of the system without forces acting on it could serve as a reference. If forces (e.g. species removals) are now applied to the system, then departure from this reference trajectory could be a measure of the intensity of the forces. The fish abundances measured over the three year period in the the Millstream were assumed to reflect the natural variability of our pristine system, without the force of species removal acting on them. Fish abundances as state variables were displayed in one point for every seasonal community through MDS-ordination (Figure 4.2). These resulting nine points could now be interpreted as boundaries for the domain of attraction. If the communities that were subject to species removals were to fall outside these boundaries (i.e. their distance to the Baseline Model would be larger that the distance between the Baseline Model and the observed communities), then, per definition, a system shift would have occurred. The results from the MDS ordination suggested that the system is resilient to single species removal. Our model system is defined by low stability, but high resilience (Holling, 1973). Low stability, because the abundance of species fluctuated to a certain degree within years and within seasons (Figure 4.2), with some of the fish species not always present. High resilience, because the defined boundaries (domain of attraction for the ecosystem), were not crossed by the communities that experienced species removals. Since none of the removal communities were outside the boundaries, it was concluded that further analysis (e.g. testing for significant differences between the removal communities and the Baseline Model) was not adding to the understanding of the system. Additionally, the judgement of potential system shifts

with the applied method was preferred to testing for significant differences between communities because statistically significant communities might not have ecological meaning. For example, a popular method in community ecology for analysing community similarities is ANOSIM (Analysis of similarities). However, ANOSIM was not found suitable because, firstly, removed species enter the analysis as zero values in contrast to the MDS, in which the removed species is omitted from the analysis for each pair that is compared. As a consequence ANOSIM will detect differences between the communities that are based on the species removal and not solely on the remaining species abundances. Secondly, significant (or not significant) results still need to be placed in a context that is ecologically meaningful, which, in this case, was achieved by putting the results of the removals in context with the natural variability of the system.

The results of the present study also support the findings of Eklof and Ebenman (2006), who found that most secondary extinctions are due to direct bottom-up effects. Here, the only secondary extinctions were caused by the removal of prey nodes, which are a large proportion of most fish diets. Roach went extinct after Ephemeroptera and Trichoptera removal. Although the consumption rate on other prey nodes was raised to match the predators ingestion rate when one of its prey species was removed, in this case the energy supply was not sufficient to support Roach. The question remains, why only one node suffered secondary extinctions, whereas other nodes (e.g. Bullhead and Dace) that also strongly depended on the same prey nodes and experienced higher predator pressure did not. Roach and Gudgeon are the only nodes that did not receive additional energy input (*cf.* Chapter 3) and Gudgeon also showed a large decrease (50%) after the removal of its main energy source (Gammaridae). The model system receives constant input from the environment, which was needed to achieve a stable system that resembles the natural community closely enough. The additional energy input might stabilise the other fish nodes (O'Neill, 1976), with the effect from the removal of their prey nodes potentially weakened.

The removal of the top predators Pike and Eel resulted in communities most

dissimilar to the Baseline community, although still within the proposed reference boundaries. Predator removal can elicit a trophic cascade (Polis et al., 2000; Borer et al., 2005; Schmitz, 2006; Hall et al., 2007) and induce system shifts (Power, 1990; Scheffer, 1990; Carpenter and Kitchell, 1996; Scheffer et al., 2001). In our system, Pike removal had a positive effect on Eel and vice versa and in both cases, prey nodes were released from predator pressure and increased in abundance. In particular, Eel mainly preys on Bullhead, whereas Pike mainly preys on Minnow, followed by Dace and Gudgeon. Eel removal was followed by a large increase in Bullhead abundance and smaller decreases in Dace and Gudgeon abundance, whereas Pike removal was followed by an increase in Gudgeon, Minnow and Dace and a decrease in Bullhead. These results are in accordance with findings that a second predator can mediate predator impact (Worsfold et al., 2009) and that more diverse predator guilds are more effective in exploiting the available resources (Nilsson et al., 2008). A dampening effect of predator diversity on trophic cascades has also been found for terrestrial systems (Finke and Denno, 2004). Comparative studies of predator removal experiments in cages found that the strength of predator impacts was dependent on the magnitude of prey exchange rates between the cage and the surrounding environment and the spatial scale of experiments (Cooper et al., 1990; Englund, 1997). Smaller mesh size of the cages hindered prey exchange and stronger trophic cascades could be observed, whereas larger mesh sizes allowed prey exchange and observed trophic cascades were weak (Cooper et al., 1990). When the additional energy input is interpreted as immigration, observed predator impacts could potentially be dependent on the magnitude of these inputs.

Macroinvertebrate and fish node removals had different effects on secondary production. Whereas, macroinvertebrate removal generally resulted in lower secondary production, fish removal resulted in higher secondary production. In the present study, diversity could not be linked to secondary production as a measure of ecosystem function.

The Millstream food web model can be described as resilient to single species removal, although some impacts have been shown, in particular after prey removal.

Fath (2004) found that network parameters are affected by network size, i.e. they are scale dependent, which has direct consequences on the selection of system boundaries and aggregation of species. Aggregated nodes, such as macroinvertebrate families in the present study, can also have an effect on system indices that define resilience (Cohen et al., 1993; Abarca-Arenas and Ulanowicz, 2002; Johnson et al., 2009b). Detailed information on high level consumers with aggregation lower in the food web may overestimate ecosystem resilience (Pinnegar et al., 2005). Consequently the model's predictive value should increase with further resolution of the macroinvertebrate nodes. Not all members of the macroinvertebrate families share the same feeding patterns, which has been averaged for the present study. At the moment, macroinvertebrate nodes can merely be interpreted as food sources for fish. The difficulty in representing macroinvertebrate nodes in greater detail, comes from a lack of available data. However, the results emphasised the influence of prey nodes on secondary production with relevant consequences for conservation, since it highlights the importance to direct management efforts towards ensuring a healthy food supply for fishes. In addition, the influence of top predators on community composition was confirmed. Contrary to Paine's (1969b) definition of a keystone species, diversity increased relatively after the removal of one predator, but it still has to be confirmed, if the same result is found when both predators are removed simultaneously, since Paine's model ecosystem only consisted of one top predator. It is likely that top predators are the first to go extinct as a response to environmental change (Petchey et al., 1999; Duffy, 2003) and future research should incorporate sequential species deletions that are ecological meaningful to test further scenarios that might cause significant shifts. In summary, it was not possible to identify one or more keystone species with the applied modelling approch for this ecosystem. None of the removals caused a significant and irreversible system shift. However, some removals caused larger dissimilarities in community composition and biodiversity than others, confirming that species influence the shaping of community structure differently. The lack of keystone species could have several reasons. Firstly, the ecosystem has a high redundancy on all levels, which makes the loss of a single

species less dramatic. Secondly, the discussed factors that might have artificially increased stability in the model system (aggregation, additional energy input) could have disguised possible shifts. Thirdly, species removal might impact more severly on other aspects of ecosystem function than secondary production, which were not investigated in the current study.

Chapter 5

Impact of non-native species introductions on food web structure and biodiversity

5.1 Introduction

In the last 30 years, with growing global trade the rate of fish introduction has doubled, and with it the risk of impact on freshwater ecosystems (Gozlan et al., 2010b). The main introduction pathways are aquaculture (De Silva et al., 2006), improvement of wild stocks (Ogutuohwayo and Hecky, 1991; Gherardi et al., 2008), ornamental fish trade (Copp et al., 2005b, 2010b; Keller and Lodge, 2007; Zieba et al., 2010), and bio-control (Kumar and Hwang, 2006), but also accidental introductions have been reported (Holcik, 1991; Gozlan et al., 2002). There is a direct link between human population density and live fish imports (Copp et al., 2007, 2010a), indicating that economic and social drivers are a main driver of propagule pressure of fish introductions (Gozlan, 2008a,b; Copp et al., 2010a). Colonisation processes are no longer restricted to natural dispersal events that are inhibited by natural barriers, rather human induced movements over large spatial areas are increasingly common (Rahel, 2007). When a fish is introduced into a suitable ecosystem for their biological

and ecological requirements, their establishment is strongly correlated to propagule pressure (number and frequency of introductions; Copp et al., 2007; Gozlan, 2008b; Copp et al., 2010a). The adverse impacts of introduced species can be categorised into ecological and socio-economic effects, though the socio-economic benefits are generally perceived to outweigh the ecological adverse effects (`http://www.fao.org/fishery/en`).

Aquaculture and ornamental fish trade (Copp et al., 2005a, 2010b; Rixon et al., 2005; Duggan et al., 2006; Zieba et al., 2010) are driven by the associated financial benefits of these businesses. Aquaculture is probably the fastest growing business in the food sector (FAO, 2008). Almost half of the world's food fish is presently produced in aquaculture (Duarte et al., 2009). The U.K.'s aquaculture production showed a steady increase from 30 to 888 tonnes per year between 1950 and 1978, followed by a massive rise to the current 174 203 tonnes per year, with a total value of Â£581 million (FAO, values from 2007). The recreational fishing industry across Europe is worth over Â£22 billion per year (Arlinghaus et al., 2002; Cooke and Cowx, 2004). In Great Britain, an estimated 3.3 million recreational anglers spent a total of Â£3.3 billion pounds annually on fishing (NRA, 1994; Lewis, 2004). The international ornamental fish industry is worth an estimated Â£9.4 billion(FAO, 2008), including wages, retail sales and associated materials. Jobs are created in export and import countries, and especially developing countries rely on harvesting ornamental species in areas where there are little opportunities for other sources of income.

Except for intentional stocking of recreational fisheries, non-native fish used in aquaculture and for ornamental purpose tend to be kept in closed systems with relatively high bio-security measures in place to limit escape and subsequent dispersal. Despite these measures, escapees (accidental and intentional) are a relatively common phenomenon, increasing the likelihood of their colonisation and subsequent establishment (Copp et al., 2005d). Although ornamental warm water species (thermal optima > 28°C) are unlikely to be able to establish in the wild in temperate regions, cold water (thermal optima < 20°C) and cool-water (thermal optima between

20 to 28°C) fishes may survive and establish, particualarly in Southern England (Britton et al., 2010a). Fish that survive, but do not establish due to temperature constraints, may benefit if thermal inhibitions dimish through climate warming and so their establishment may still occur but be subject to a lag phase (Britton et al., 2010a). Where non-native escapees have dispersed into the wild, colonised new waters and established sustainable populations, adverse ecological consequences may be incurred (Gozlan et al., 2010b). It is thus important to develop predictions of potential ecological impacts following their introductions. The key ecological impacts that may be associated with non-native fish in the environment are: habitat degradation (Miller and Crowl, 2006), hybridisation (Hanfling et al., 2005), disease transmission (Blanc, 1997; Gozlan et al., 2005; Gozlan, 2008b), and impacts on food web structure though predation and competition (Townsend, 2003).

There is an ongoing debate on how an ecological impact through non-native fish introductions may be best defined and measured, since impacts are not always obvious or immediate (Gozlan, 2008b; Leprieur et al., 2009; Gozlan et al., 2010b). Opinions on allowing intentional introductions to proceed range from precautionary, risk averse approaches where only species that are predicted to have only minimal impact on their new environment can be introduced ("guilty until proven innocent" approach; Sandin, 1999; Leprieur et al., 2009) to the call of introducing species to replace those lost as a consequence of environmental change (Sagoff, 2005; Simberloff, 2007; Gozlan, 2008b). This debate is, however, crucial in the context of fish introductions in that once in the environment, they are very difficult to manage (Britton et al., 2011). Although preventing all introductions may appear to provide the safest approach from an ecological viewpoint (Sandin, 1999), one has to consider the afore-mentioned societal and economic benefits that may occur and the possibility that carefully chosen introductions may even be ecologically beneficial. For example, a greatly disputed case of a benefical or detrimental invader that resulted from an accidental introduction is the zebra mussel (*Dreissena polymorpha*) in the North American Great Lakes (Strayer, 2009). While the introduction had a highly negative economical impact (e.g fouling of water intakes and boats; Strayer,

2009; Vitule et al., 2009), it has also been argued that the degraded, eutophicated state of the Great Lakes have been improved by zebra mussel presence through their filtration of the water, resulting in decreased turbidity, increased benthic macroinvertebrate diversity, and has become an important food source for fish and birds (Sagoff, 2007; Gozlan, 2008b). Although non-native species introductions have been associated with biodiversity loss, other drivers, such as habitat modification and management practices tend to be correlated, leaving the main cause of biodiversity loss often unclear (Didham et al., 2005). In these situations, successful management of the invader may not restore the ecosystem to its pre-invasion state (Britton et al., 2011).

There are several possible outcomes of invasions. Native species might be replaced by the invader (Dick et al., 1993; Townsend, 2003), or co-exist (Eby et al., 2006); and ecosystem processes may be altered (Wikramanayake and Moyle, 1989; Power, 1990; Gurevitch and Padilla, 2004). For example, whilst the introduced *S. trutta* replaced native galaxiid fishes in some New Zealand streams, the food web structure did not change (McIntosh and Townsend, 1995). However, the more voracious predatory *S. trutta* caused a trophic cascade by changing the foraging behaviour of its macroinvertebrate prey. These became more nocturnal, resulting in reduced algal grazing and consequently higher algal biomass (McIntosh and Townsend, 1995). Another example of an invading top predator is the dragonfly larvae *Cordulagaster boltonii* (Woodward and Hildrew, 2001). After its invasion of a small stream, changes in food web structure consisted of increased mean food-chain lengths, web complexity and omnivory. However, there was little evidence for top-down control of prey abundance and, consequently, primary production. These examples illustrate that impacts of invasions cannot be determined solely by assessing changes to food web structure or by the trophic position the invading species will occupy.

To oversee such issues, dynamical modelling approaches can potentially capture impacts on community composition (abundance of species) after species introduction, not only changes in food web structure (e.g. link density, food chain length, see Chapter 2). As the *S. trutta* example illustrates, behavioural adaptions can occur,

and these are impossible to integrate in modelling approaches without further, often uncertain, assumptions being used. Changes in community composition and structure after introductions can therefore be mitigated or amplified by additional factors, which has to be considered when results are interpreted. For example, one of the model species that is introduced into the food web is also a healthy carrier of a pathogen that affects native species, posing an additional threat on the native fish community (this is discussed in more detail below).

Consequently, this chapter focuses on the potential consequences of species introductions on energy distribution in the food web of the River Frome, while excluding impacts that are caused by habitat degradation or land use change. This will be achieved by adding three model species to the Baseline Model, introduced in Chapter 3, at different densities and assessing consequent changes in biodiversity and community composition.

Aims and objectives

The aim of this chapter is to evaluate, using the dynamical food web model, the impacts of introductions of non-native fishes on energy distribution.

Objectives are to:

1. Identify changes in the dynamical food web model as a consequence of introducing three model species, representing introductions with different characteristics.

2. Evaluate the impacts of the introductions through measuring changes in community composition and biodiversity.

5.2 Material and Methods

5.2.1 Ecology of the the three model species

Non-native and non-indegenous fishes present in nearby river catchments, but not yet found in the River Frome include barbel (*Barbus barbus*), topmouth gudgeon (*Pseudorasbora parva*) and pikeperch (*Sander lucioperca*); the latter two species being non-native, whereas barbel is native to eastern England river catchments. Those three model species have been chosen because, firstly, they have successfully established breeding populations in other parts of the UK, suggesting that they could establish in the Frome catchment as well. Secondly, they represent fish entering the food web at different trophic levels. Thirdly, *S. lucioperca* and *B. barbus* are of interest to anglers, therefore an introduction could potentially be considered to add economic value to a river, whereas *P. parva*, is considered a nuisance species that could be accidently introduced because of its size and has caused considerable economic damage through costly removal programmes in other parts of the UK (Britton et al., 2008, 2010b). Finally, *P. parva* and *S. lucioperca* have been found to impact on native fauna, whereas impacts after the introduction of *Barbus spp.* in other European countries could not be identified. The diets and feeding rates are based on characteristics of those three model species, regarding trophic position, diet composition and body size. *P. parva* and *B. barbus* are at an intermediate level in the food web. Although they share a similar trophic position, their mean body sizes differ with this then reflected in their ingestion rates, as smaller bodied organisms have a higher ingestion rate per gram body weight than larger individuals (Peters, 1983). Therefore, the same biomass of the smaller species could possibly have a larger effect on food resources and consequently food web structure. While the diet of *B. barbus* was based on gut content analysis found in literature, the diet of *P. parva* was intentionally implemented as very similar to gudgeon (*Gobio gobio*) diet to imitate competition. *S. lucioperca* is chosen as an example of the introduction of an apex predator to investigate possible top-down effects. As in the previous chapters, CAPITAL letters are used to refer to the nodes in the dynamical food web

(i.e. Barbel, Pikeperch, TopGug) to avoid confusion with the actual species.

S. lucioperca (pikeperch)

S. lucioperca (Percidae) is non-indigenous to the UK (Wheeler and Maitland, 1973). A piscivorous fish native to Central and Eastern Europe, they have been successfully introduced to Western Europe, Western Turkey and Morocco (Lappalainen et al., 2003). Although initially introduced to Eastern England in the mid/late 1800s by the Duke of Bedford for angling purposes their now widespread dispersal *via* human movements to other open waters was in 1950s and 1960s, and included stockings to the Greater Ouse Relief Channel in 1963. They then colonised some neighbouring parts of the River Great Ouse (Linfield and Rickards, 1979; Hickley, 1986). *S. lucioperca* prefers either deeper lacustrine waters or turbid shallow waters, with riverine populations usually inhabiting slow flowing area with little or no vegetation (G.H. Copp, pers. com.). Maximum length has been reported as 100cm (FL, Kottelat and Freyhof, 2007), and common length as 50cm (FL, Muus and Dahlström, 1968). Their temperature range lies between 6°–22°C (Baensch and Riehl, 1991). Adverse effects by introduced *S. lucioperca* on native fish populations have been reported (Welcomme, 1988) but rarely substantiated (Smith et al., 1998). The simultaneous reduction of cyprinid numbers and establishment of *S. lucioperca* has led to the instigation of removal programs (culling) to preserve prey fish population abundance (Smith et al., 1996). However, more recent research concluded *S. lucioperca* were not the cause of their decline (Smith et al., 1998). Kopp et al. (2009) found that invading *S. lucioperca* in France occupy a higher trophic position than other predatory fish, such as *E. lucius*, hence possibly directly influencing predator abundance by predation and not only through competition. Their diet consists mainly of omnivorous fish, but other predatory fish, such as small *E. lucius*, and macroinvertebrates, such as *Asellus aquaticus* and *Lumbricus terrestris*, are also taken (Smith et al., 1996). In the North Oxford canal, their diet mainly comprised *C. gobio* and *R. rutilus*, although $\approx$ 33% of prey fishes were unable to be identified (Smith et al., 1996). In the food web model, it will be assumed that *S. lucioperca* will feed on all other

fish species present to reflect their high trophic positions reported in the literature (Kopp et al., 2009).

B. barbus (barbel)

B. barbus (Cyprinidae) thrive in fast-flowing rivers and streams, although also found in lacustrine habitats in the UK, these populations have to be maintained by stocking (Taylor et al., 2004). Indigenous to rivers on the eastern side of England (Yorkshire to Kent), *B. barbus* have been translocated to a number of UK rivers outside of this range, including the Dorset Stour and the Sussex Ouse in Southern England to the River Clyde in Scotland, for recreational angling purposes as they are a popular sport fish (Wheeler and Jordan, 1990; Taylor et al., 2004). In UK rivers, *B. barbus* generally achieve a maximum length of 60 cm (FL), although elsewhere specimens up to 120 cm (FL) and >10 kg have been encountered (Bianco, 1998). A benthivore, *B. barbus* feed primarily on crustaceans and other macroinvertebrates, but small fish are sometimes taken (Kottelat and Freyhof, 2007). Individuals generally remain within a home range of <20 km with seasonal migration patterns (Lucas and Batley, 1996; Vilizzi et al., 2006), but have also been observed to migrate long distances (>300 km; Schreiber, 2009). Optimal temperatures for growth range between 10° and 18°C (Davies and Quill, 2004). Spawning takes place in late spring and the early summer, when water temperatures reach 18°C (Varley, 1967; Hancock et al., 1976; Baras, 1994). Males usually mature after three, and females after five years (Maitland and Campbell, 1992). Given the successful translocations of *B. barbus* for angling purposes (Wheeler and Jordan, 1990), further introductions to other catchments are likely, despite being aganst fish movement legislation (Hickley and Chare, 2004). Furthermore, there is little information of the ecological impacts caused by translocated, non-indigenous *B. barbus* in the UK. As their translocation into the River Frome remains a possibility they represent a realistic candidate as a translocated fish for this study.

P. parva (topmouth gudgeon)

P. parva (Cyprinidae), native to China, Korea, Japan and the River Amur basin, was accidentally introduced into the lower River Danube basin in Romania in the 1960s and has subsequently spread rapidly throughout Europe (Pinder and Gozlan, 2003; Gozlan et al., 2010a). It has been present in the wild in the UK since at least 1996 (Domaniewski and Wheeler, 1996), but was introduced on to an aquaculture site in 1985 (Pinder et al., 2005). Although their maximum size is $\approx$ 100 mm, the majority of fish in a population will be $<$ 60 mm (FL; Britton et al., 2010c). Maturity is generally reached after only a year, and the total lifespan is between four (Gozlan et al., 2010a) to five years (Novikov et al., 2002). Habitat preferences are for shallow lakes, ponds, ditches and slow flowing sections of lowland rivers with high vegetation. The diet consists mainly of algae, benthic invertebrates, zooplankton, eggs and larval stages of other fish (Gozlan et al., 2010a). Small *P. parva* mainly prey on cladoceran zooplankton species, and larger individuals have been found to feed mainly on chironomids (Gozlan et al., 2010a). *P. parva* populations can be encountered in high densities, raising concerns of inter-specific competition with native fishes (Witkowski, 2006; Britton et al., 2010c). *P. parva* was also found to be a healthy carrier of the rosette agent *Sphaerothecum destruens* (Gozlan et al., 2005, 2009), which has affected salmonid species in North America and possibly sunbleak (*Leucaspius delineatus*) across Europe (Gozlan et al., 2010a). The pathogen causes a chronic disease, making it difficult to characterise in wild populations, despite causing mass mortality, and is considered a major threat to fish biodiversity (Gozlan et al., 2005). Given the known high densities of their invading populations and potential for competition (Britton et al., 2010c), this is the aspect of interest when they are introduced into the food web model. Moreover, with higher ingestion rate per gram body weight than larger fish (Peters, 1983), they may deplete energy sources faster.

5.2.2 Introduction densities for the three model species

The model species are introduced at different starting abundances to simulate different propagule pressures. Pikeperch and Barbel are introduced at three different densities, whereas TopGud is introduced at four different densities. It is also assumed that all species are preyed on by Pike and Eel. The impact of the introductions on diversity is assessed by comparing the Shannon Index of the communities. Community shifts are also assessed by comparing Bray-Curtis coefficients.

Introduction of Pikeperch

The starting densities for PIKEPERCH (Table 5.1) were equivalent to introducing 2, 24 and 60 individuals, each weighing ≈ 100 g, into the 1200 m^2 study area. This weight of individual was used as it represents their mean weight in a UK population (North Oxford Canal; Smith et al., 1996). Their starting densities were guided by densities found for *E. lucius* for the Millstream (*cf.* Chapter 3). In the Baseline model, PIKE is introduced in three size classes. The sum of the starting stock value of all PIKE is 5500 cal/m^2, whereas the large size group PIKE3 (>2 kg) contains 4100 cal m^{-2}. PIKE1 (≈ 100 g) has a starting value of 270 cal m^{-2}, equivalent to a density of 0.002 individuals per m^2. This density was chosen as the lowest introduction density for PIKEPERCH, whereas the medium and high abundances reflected values lower and higher than of the total PIKE abundance. The diet composition (Figure 5.1) was based on gut content analysis from Smith et al. (1996). PIKE1, PIKE2, PIKE3, and EEL_2 and EEL_3 predated moderately upon PIKEPERCH.

Table 5.1: Introduction abundances for PIKEPERCH.

Introduction density	Introduction density [ind m^{-2}]	Starting stock value [cal m^{-2}]
low	0.002	346
medium	0.020	3114
high	0.050	7784

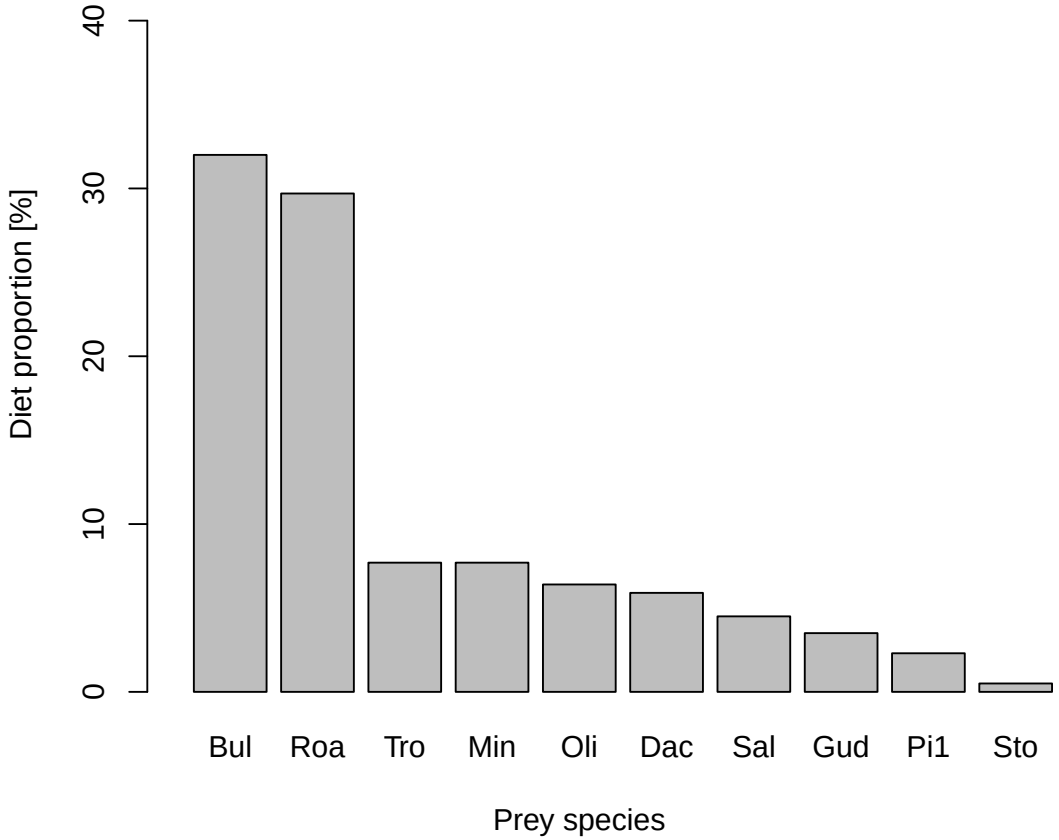


Figure 5.1: Proportionate diet composition for Pikeperch, which receives most of its energy from the nodes Bullhead and Roach. For abbreviations of prey nodes see Appendix Table A.3.

Introduction of Barbel

The starting values for Barbel (Table 5.2) were equivalent to introducing 6, 60 and 90 individuals respectively, each weighing $\approx$ 60 g, to the 1200 m^2 study area. This individual weight was chosen as it is similar to the mean weight calculated for *L. leuciscus* and *R. rutilus* from the Millstream data (Appendix, Table A.3). The introduction densities were based on the measured abundance of *G. gobio* (low introduction density) and *L. leuciscus* (high introduction density), because those were the cyprinids with the measured lowest and highest abundance (AppendixTable A.3). Given the scarcity of literature on *B. barbus* diet in the UK (Copp et al., 2005c for young of the year *B. barbus*), the diet of Barbel was based on the diet composition of Iberian *B. barbus* (*Barbus bocagei*) described in Collares-Pereira et al. (1996). Although Barbel was similar sized and therefore had a similar ingestion rate as Roach and Dace, Barbel mainly fed on Diptera, compared to the other two fish nodes, which receive their energy mainly from Diptera, Gammaridae and Trichoptera. Pike1, Pike2, Pike3, and Eel_2 and Eel_3 prey upon Barbel in a similar manner as those predators prey on Roach, Gudgeon or Dace, species nodes of similar size.

Table 5.2: Introduction abundances for Barbel.

Introduction density	Introduction density [ind m^{-2}]	Starting stock value [cal m^{-2}]
low	0.005	448
medium	0.050	4479
high	0.075	6719

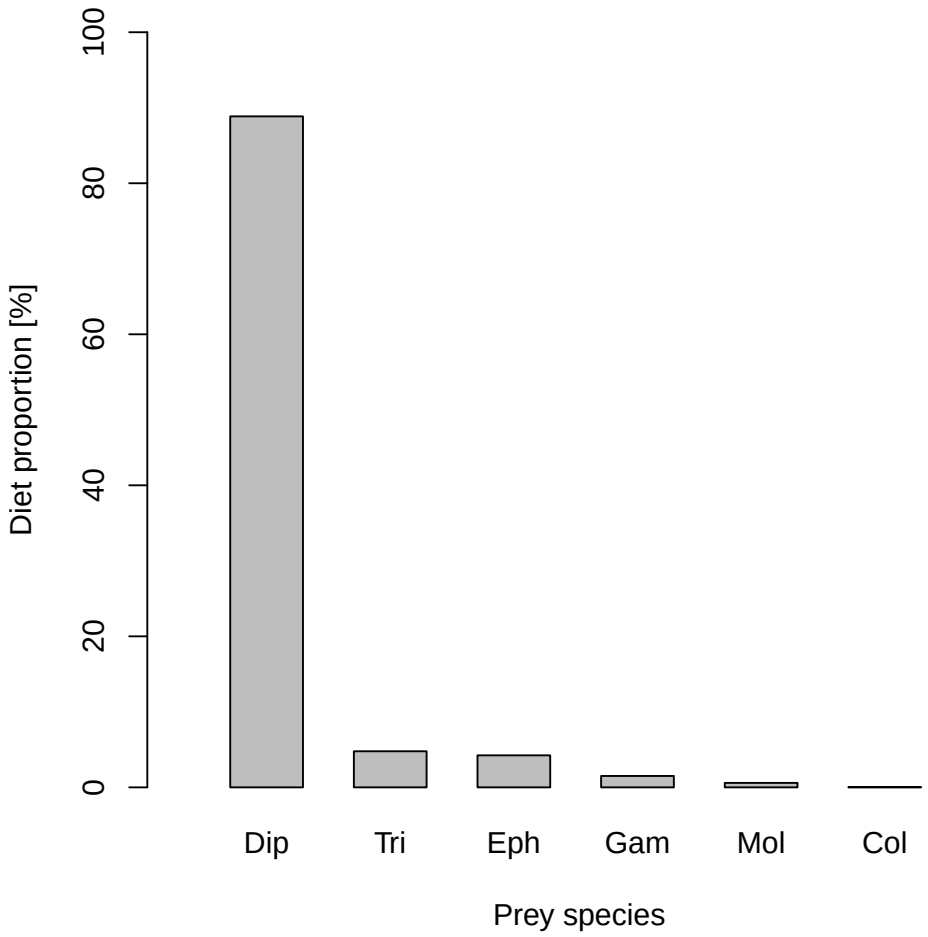


Figure 5.2: Proportionate diet composition for Barbel. Almost all energy is received from the node Diptera. For abbreviations of prey nodes see Appendix Table A.3.

Introduction of TopGud

The starting values for TopGud (Table 5.3) were equivalent to introducing 240, 600, 1200, and 2400 individuals, each weighing $\approx$ 1 g to the 1200 m^2 study area. The mean weight was chosen based on the assumption that the mean individual would have a fork-length between 3 cm (approximate size that maturity is reached) and 8 cm (common length, Berg, 1964). The low introduction density chosen was slightly less than the starting stock values of Gudgeon and then doubled respectively. As *P. parva* has been reported to occur in very high densities (Britton et al., 2010c; Gozlan et al., 2010a), then it is also introduced at an additional, higher density. In the Baseline Model, Minnow has the highest density with approximately 1 ind. m^{-2} (2272 cal m^{-2}). This density is doubled for TopGud (very high density). The diet composition of TopGud is closely matching the diet composition of Gudgeon, consisting of Diptera, Gammaridae and Trichoptera. This choice is justified as although found for a pond community, *P. parva* and gudgeon do not have significant differences in their diet (Declerck et al., 2002). The values for body size and the diet composition has been chosen to simulate a competitor with higher ingestion rates per gram body weight, with a similar diet composition compared to gudgeon. For other nodes, Diptera, Gammaridae and Trichoptera also formed an important part of the diet (e.g. Minnow, Stoneloach, Salmon and Trout), but in different proportions. Pike1, Pike2, Pike3, and Eel_2 and Eel_3 preyed on TopGud in a similar manner as Minnow and Bullhead, since those fish were of similar size as the introduced node.

Table 5.3: Introduction abundances for TopGud.

Introduction density	Introduction density [ind m^{-2}]	Starting stock value [cal m^{-2}]
low	0.2	299
medium	0.5	747
high	1.0	1493
very high	2.0	2986

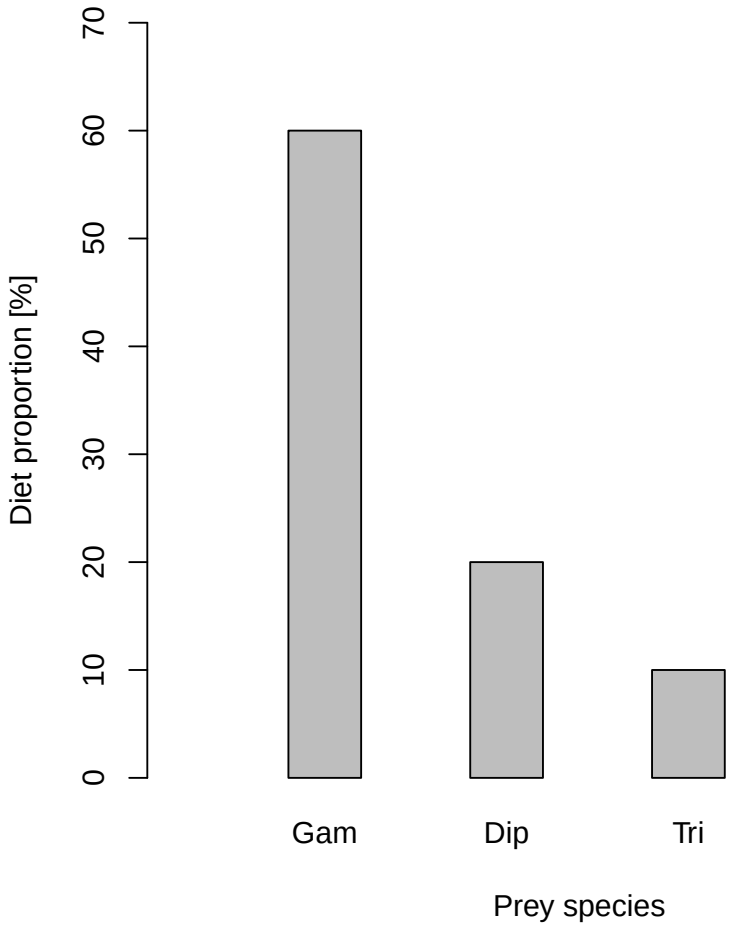


Figure 5.3: Proportionate diet composition for TopGud. Most of the energy is received from the node Gammaridae. For abbreviations of prey nodes see Appendix Table A.3.

5.3 Results

Introduction of Pikeperch

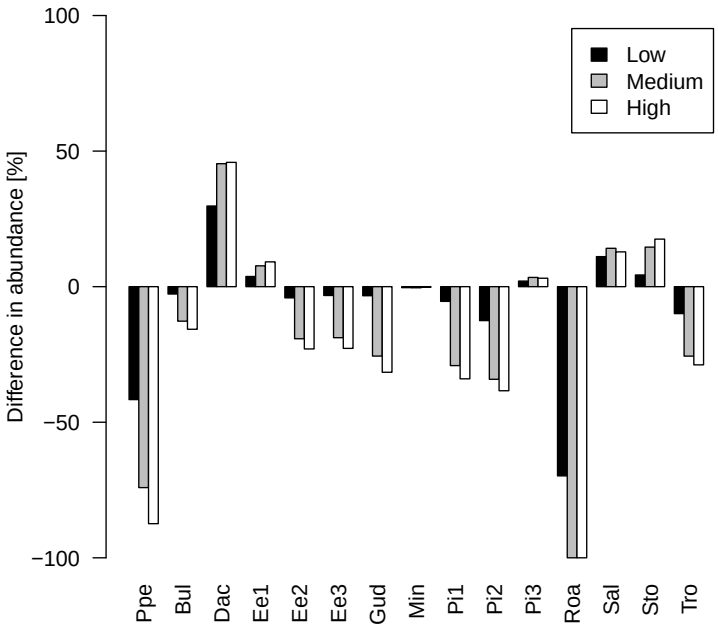
In general, the impacts of Pikeperch introduction were stronger with increased number of introduced individuals. Their introduction caused a decrease in species diversity, which was calculated for the entire community, including with and without Pikeperch. As introduction density increased, diversity declined (Table 5.4). Eight of the 14 fish nodes showed a decrease after introduction, with Roach going extinct at the medium and high introduction density (Figure 5.4). A large increase (50%) was apparent for Dace. Pikeperch mainly had a negative effect on its prey nodes, but also on other top predators, namely Eel 2, Eel 3 and Pike2. Although both Bullhead and Roach form the largest part of the Pikeperch diet ($\approx 30\%$ each), the nodes were affected differently. Bullhead abundance was less affected, while Roach declined to extinction. The abundance of macroinvertebrate nodes was hardly affected with the exception of the increased abundance of Ephemeroptera. In all cases the final stock values of Pikeperch were also substantially lower than the introduction densities.

Table 5.4: Shannon-Diversity Index (H') for the communities after the introduction of Pikeperch at different densities. The values in brackets are the effective number of species (true diversity, exp (H')).

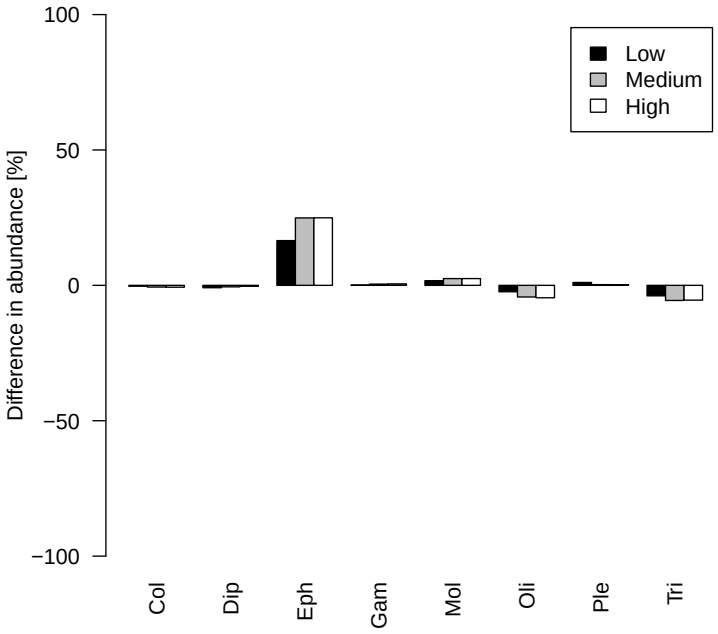
Community	H' (exp (H'))	H' without Pikeperch abundance (exp (H'))
Pikeperch high	2.43 (11.4)	2.37 (10.7)
Pikeperch medium	2.44 (11.5)	2.38 (10.8)
Pikeperch low	2.50 (12.2)	2.48 (11.9)
Baseline Model	2.54 (12.7)	

The community shift, measured by the Bray-Curtis coefficient, revealed that with rising introduction densities the distance between the Baseline Model and the re-

sulting communities became larger (Figure 5.5). The result was not due to the effect that the addition of a node would have in making the community more dissimilar, even when the remaining abundances remained the same, since nodes that are not present in one community are not included in the calculation of the Bray-Curtis distance measure. Out of the three model species, PIKEPERCH is the only one that caused an extinction (ROACH, at medium and high density) after introduction.



(a)



(b)

Figure 5.4: Impact of Pikeperch (Ppe) introduction at different densities on the abundance of fish nodes (a) and macroinvertebrate nodes (b) in relation to the final values of the Baseline model. The values for Pikeperch are in relation to its respective starting stock values. For abbreviations see Appendix Table A.3.

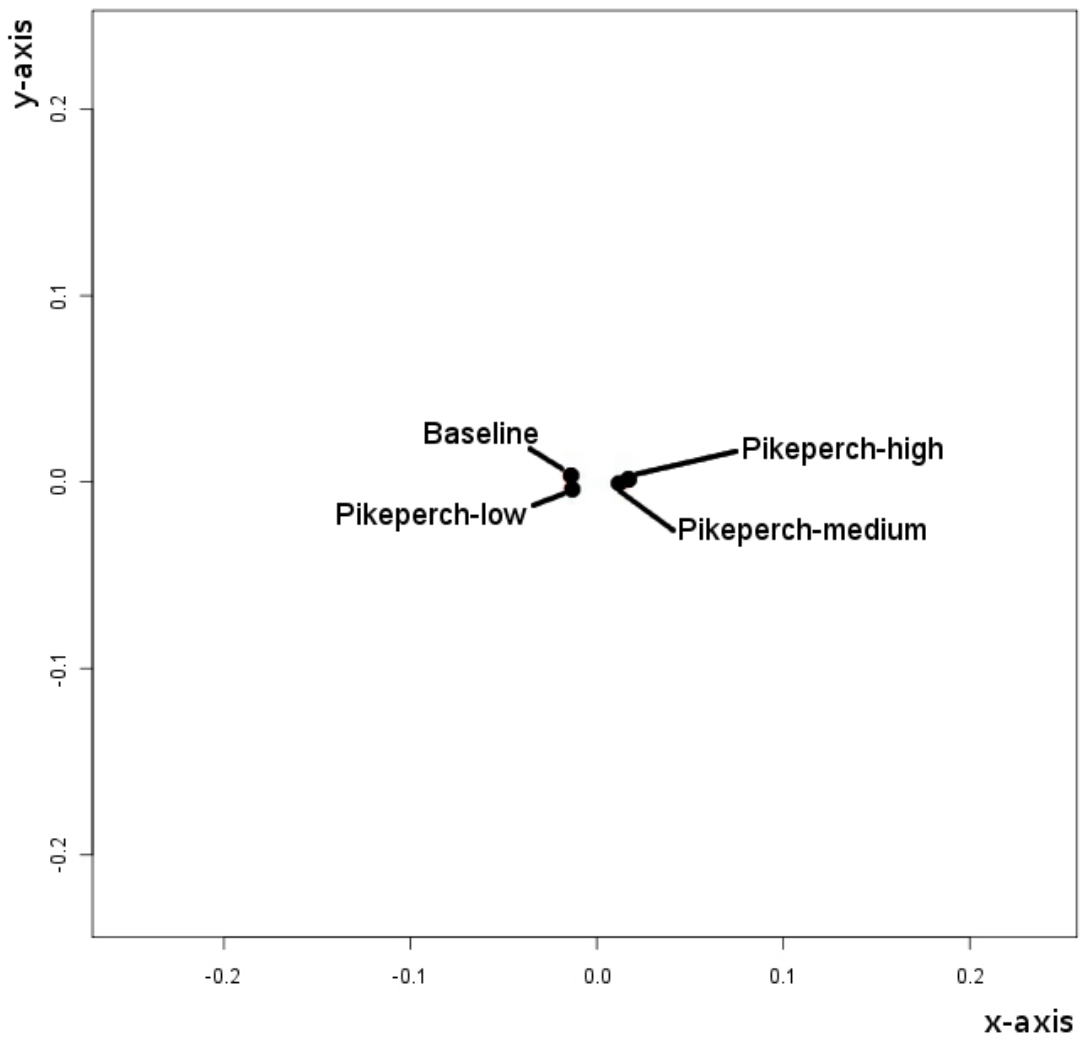


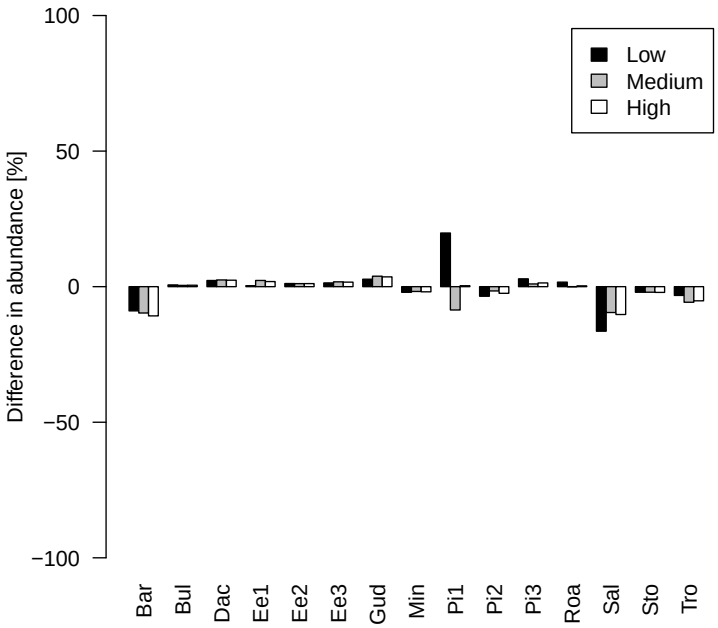
Figure 5.5: MDS ordination for the resulting communities after Pikeperch introduction. The points mark the distance of the communities resulting from different introduction densities (low, medium and high) to the Baseline Model. The axis are dimensions. Stress: 0.00%

Introduction of Barbel

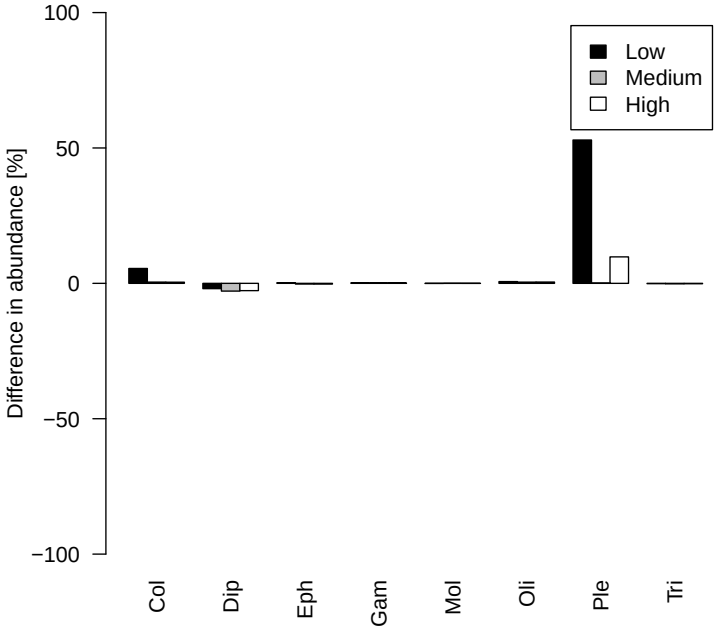
The introduction of Barbel had little impact on the food web at all introduction densities. The Shannon Index slightly increased, as would be expected when a species is added to the community (Table 5.5). No difference was found to the Shannon Index calculated without Barbel abundance. Barbel introduction had a positive effect on Pike1 at low introduction density, but negative at medium introduction density (Figure 5.6). Salmon decreased, but the decrease is larger at low introduction density. The increase in Plecoptera appears very large (Figure 5.6), but the node had a very low starting abundance (0.7 cal m^{-2}) and only increased to 1 cal m^{-2}. The final stock values of Barbel were slightly lower than the starting stock values in all three cases. There was no trend towards a community shift recognisable in the MDS graph (Figure 5.7). The resulting communities all have a similar distance to the Baseline Model.

Table 5.5: Shannon-Diversity Index (*H'*) for the communities after the introduction of Barbel at different densities. The values in brackets are the effective number of species (true diversity, exp (*H'*)).

Community	*H'* (exp (*H'*))	*H'* without Barbel abundance (exp (*H'*))
Baseline Model	2.54 (12.7)	
Barbel high	2.56 (12.9)	2.56 (12.9)
Barbel low	2.57 (13.1)	2.57 (13.1)
Barbel medium	2.60 (13.5)	2.60 (13.5)



(a)



(b)

Figure 5.6: Impact of Barbel (Bar) introduction at different densities on the abundance of fish nodes (a) and macroinvertebrate nodes (b) relative to the final values of the Baseline model. The values for Barbel are in relation to its respective starting stock values. For abbreviations see Appendix Table A.3.

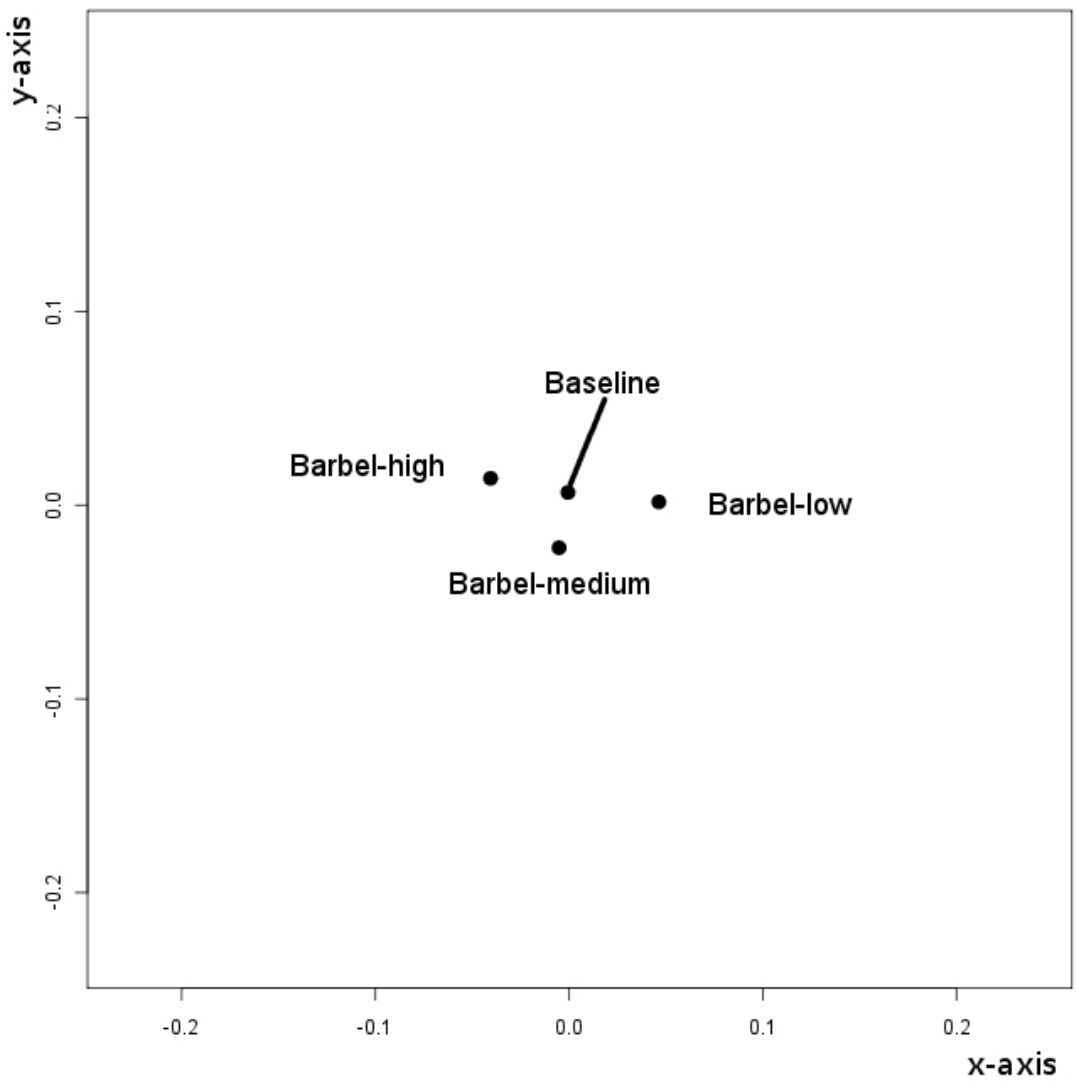


Figure 5.7: MDS ordination for the resulting communities after Barbel introduction. The points mark the distance of the communities resulting from different introduction densities (low, medium and high) to the Baseline Model. The axis are dimensions. Stress: 0.00%

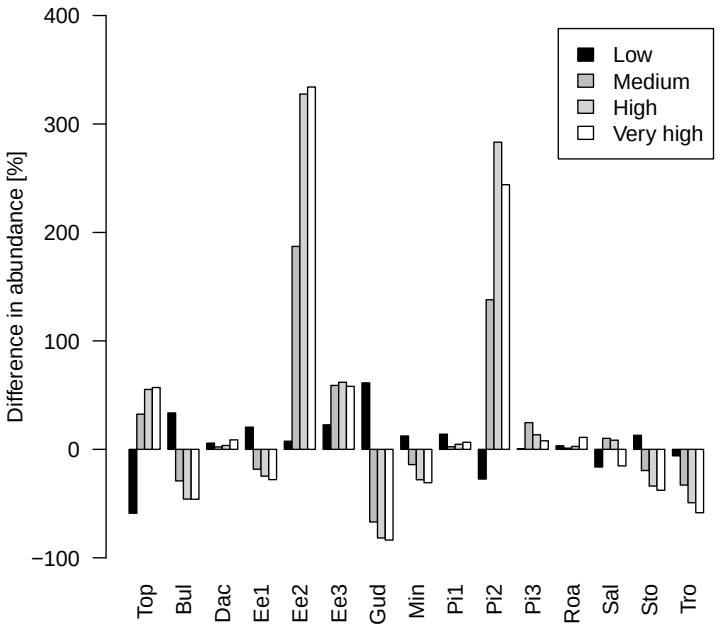
Introduction of TopGud

The introduction of TopGud caused a slight increase of the Shannon Index, similar to the Introduction of Barbel (Table 5.6), but the impact on the abundance of other nodes and the community shift, as measured by the Bray-Curtis coefficient, was severe. When the Shannon Index was calculated without TopGud abundance, diversity was lower for the high and very high introduction density. TopGud introduction had a large positive effect (up to 350%) on the abundance of its predators Eel 2 and Pike 2, while the nodes Bullhead, Eel 1, Gudgeon, Minnow, Stoneloach, Trout, and Gammaridae showed a decrease at higher introduction densities (Figure 5.8). At the low introduction density, effects were either small or even opposite. Gudgeon abundance declined to almost extinction in the scenarios with higher introduction density. Similar trends were observed for Minnow and Trout and Stoneloach, all nodes that received the most energy input from the nodes Diptera, Gammaridae and Trichoptera. The final stock values of TopGud decreased for the low introduction density, while a large increase could be observed all three other cases.

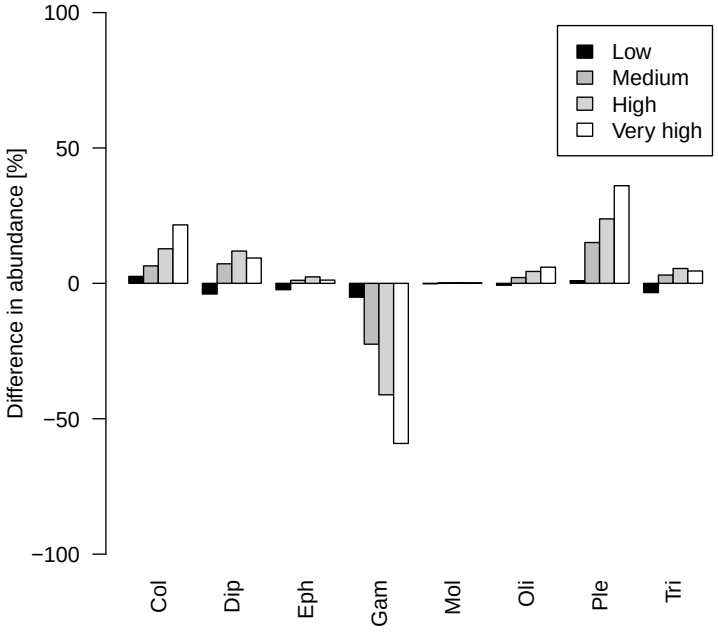
Table 5.6: Shannon-Diversity Index (*H'*) for the communities after the introduction of TopGud at different densities. The values in brackets are the effective number of species (true diversity, exp (*H'*)).

Community	*H'* (exp (*H'*))	*H'* without TopGud abundance (exp (*H'*))
Baseline Model	2.54 (12.7)	
TopGud very high	2.57 (13.1)	2.50 (12.2)
TopGud low	2.58 (13.2)	2.56 (12.9)
TopGud high	2.58 (13.2)	2.51 (12.3)
TopGud medium	2.60 (13.5)	2.54 (12.7)

The largest shift from the Baseline Model was observed after TopGud introduction at medium and high densities (Figure 5.9). The MDS graph for TopGud has a different scale to the MDS graphs for Barbel and Pikeperch introduction (Figures 5.5 and 5.7). When all communities are compared in one graph, Barbel, Pikeperch and TopGud-low could not be distinguished from the Baseline Model (Figure 5.10). Although the Shannon Index decreased more after Pikeperch introduction, this was not captured in the MDS graph.



(a)



(b)

Figure 5.8: Impact of TopGud (Top) introduction at different densities on the abundance of fish nodes (a) and macroinvertebrate nodes (b) relative to the final values of the Baseline model. The values for TopGud are in relation to its respective starting stock values. For abbreviations see Appendix Table A.3.

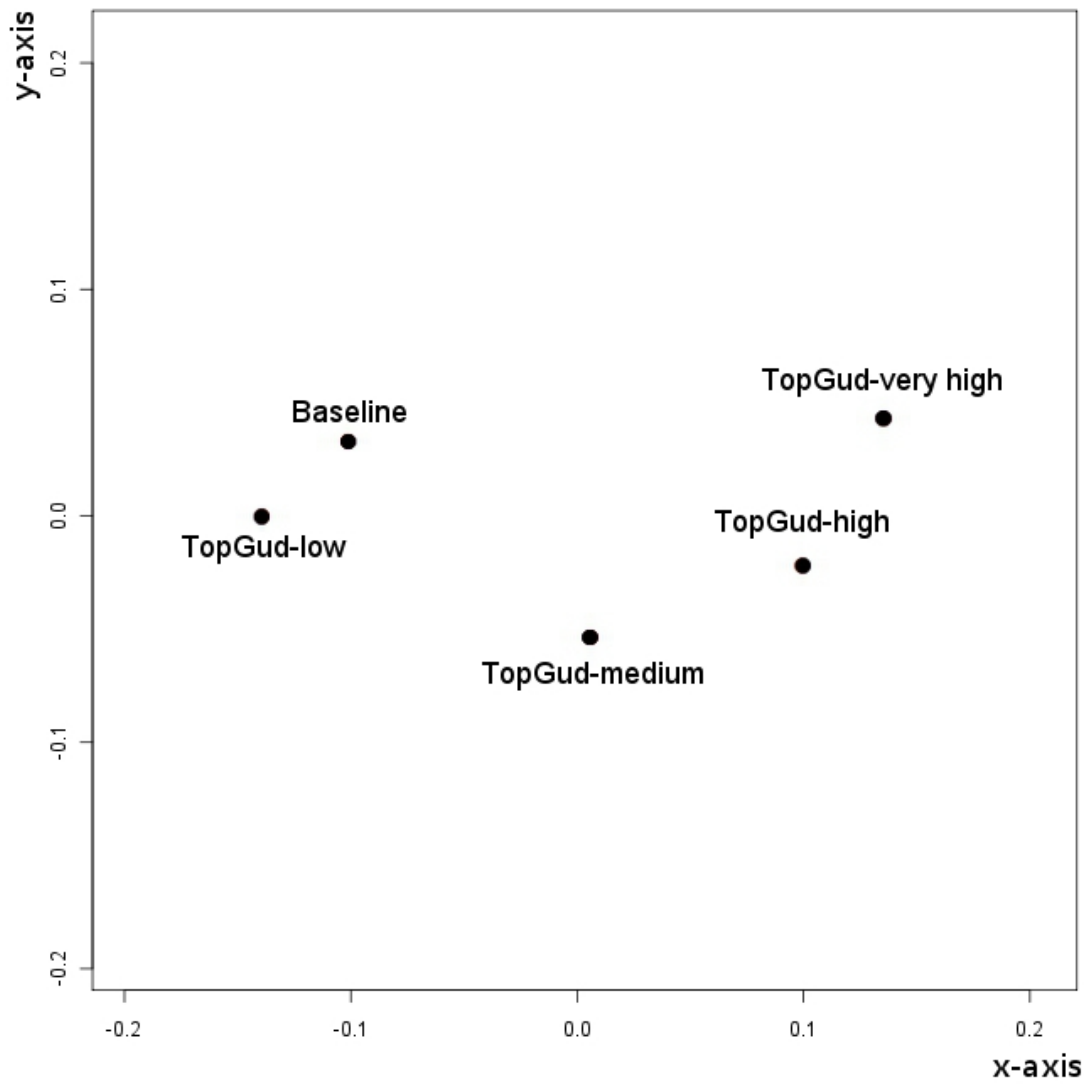


Figure 5.9: MDS ordination for the resulting communities after TopGud introduction. The points mark the distance of the communities resulting from different introduction densities (low, medium, high and very high) to the Baseline Model. The axis are dimensions. Note the scale of the axes differ to those used for Pikeperch and Barbel. Stress: 0.00%.

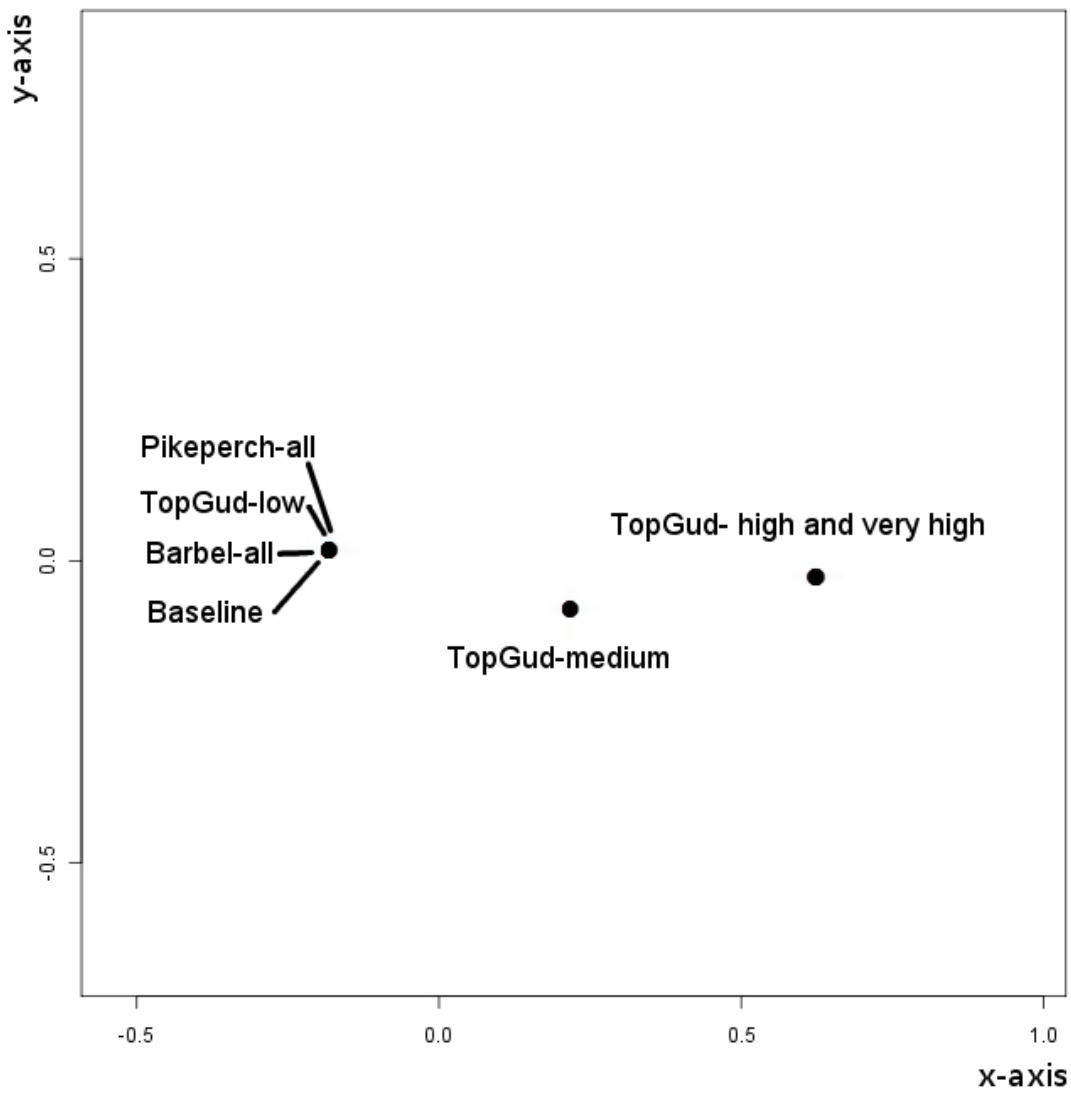


Figure 5.10: MDS ordination for all resulting communities after introductions. The axis are dimensions. On this scale the resulting communities after introduction of Pikeperch and Barbel at all introduction densities fall on one point with the Baseline Model community. The same applies to TopGud at low density. Only TopGud at higher introduction densities are different in comparison. Stress: 0.01%.

5.4 Discussion

The introduction of new species nodes into the food web model has different impacts on community structure depending on the characteristics of the introduced species. TopGud caused the greatest community shift at higher introduction densities, while Pikeperch caused the largest decline in diversity. Barbel introduction, however, did not seem to affect community structure at any introduction density.

The analysis of species introduction on the abundance of single nodes revealed that Pikeperch elicits strong top-down effects on its main prey. The results also suggested that impacts could not be deduced from the diet composition, since e.g. Dace became more abundant, although it forms about 10% of Pikeperch's diet. The main prey nodes, (Bullhead and Roach, both $\approx 30\%$) also responded differently to the introduction. Both nodes decreased, but Bullhead only decreased by $\approx 15\%$ at the medium and high introduction density, whereas Roach became extinct. The prediction of the model was consistent with findings that *S. lucioperca* can elicit a negative impact on cyprinid fish populations, such as *R. rutilus*, common carp (*Cyprinus carpio*) and common bream (*Abramis brama*) (Klee, 1981; Linfield, 1982; Smith et al., 1994, 1996). Notwithstanding, other authors have found no impact on prey fish populations (Hickley and North, 1983; Adams, 1993) or concluded that a decline in prey fish biomass cannot be attributed solely to predation by *S. lucioperca* (Leah and Kell, 1985). In a subsequent study, Smith et al. (1998) reviewed all *S. lucioperca* impact studies and found the evidence of *S. lucioperca* impacting on prey populations to be equivocal. The only apparent impact was demonstrated in an artificial environment in which an upstream and downstream section of adjacent canal stretches was compared, rather than comparing the same stretch before and after the introduction. Differences in cyprinid fish densities could therefore be explained by other, unexplored factors (Smith et al., 1998). Consequently, the model predictions contradict those findings at least at the higher introduction densities. Given the model excluded the role of environmental factors in determining impacts, then it demonstrated that the introduction of Pikeperch (or indeed other top predators)

have the potential to reduce prey fish abundance and diversity within a food web context. PIKEPERCH introduction also caused a decline in the other top predators, except PIKE3. The increases in DACE, SALMON and STONELOACH could either be due to less predator pressure from Eel and PIKE, or less competition from the other fish nodes, which decreased in abundance, or a combination of both. There is, however, no evidence for a system shift after the introduction of PIKEPERCH as measured by the Bray-Curtis distance, but the largest decrease in the Shannon Index was observed.

In a comparative study of 12 different river basins in South Korea after the introduction of the piscivorous largemouth bass (*Micropterus salmoides*), similar results to the model predictions have been found (Jang et al., 2006). *M. salmoides* populated sites had significantly lower abundance of other piscivorous predators. Four of six prey fish were also significantly less abundant, while two were significantly more abundant. Not all observed effects could be solely assigned to the presence of *M. salmoides*, since its distribution also correlates with environmental factors. Although *M. salmoides* exhibited a higher degree of piscivory in the South Korean study than in similar studies in North America, Europe and Africa, it preyed mostly on the most common prey species and was not considered a major threat to less abundant, endemic species (Jang et al., 2006). Possible diet shifts that accompany prey species abundance patterns could therefore be specific to the ecosystem to which a top predator is introduced. In regard to the interaction of *S. lucioperca* with other top predators, such as *E. lucius*, environmental factors, such as increased turbidity, which favours *S. lucioperca* (G.H. Copp, pers. com.), may pose additional influences on community composition.

A further example is the intentional introduction of piscivorous peacock bass (*Cichla kelberi*) into the Rosana Reservoir (Parana River basin, Brasil; Pelicice and Agostinho, 2009). After the introduction of *C. kelberi*, species diversity decreased severely, and after a few years, a nearly complete loss of fish assemblages was noted. The loss of prey species was described as non-linear, as large losses in biodiversity and prey abundance coincided with large shoals of young *C. kelberi* during summer,

whereas fish assemblages recovered during spring, when juvenile *C. kelberi* were absent (Pelicice and Agostinho, 2009). Potentially, juvenile *S. lucioperca* could exert similar predation pressure when introduced into the Frome catchment, adding to the impacts predicted by the food web model.

Although the starting value of TopGud (measured in cal m^{-2}) was lower at the highest introduction density than medium introduction densities for Barbel and Pikeperch, TopGud introduction had the largest impact at higher introduction densities according to MDS analysis. In response to the introduction of TopGud, nodes with similar diet composition decreased, while some of the top predator nodes increased (Eel_2, Eel_3, and Pike2 showed particularly large increase). Gudgeon abundance declined to almost extinction in the scenarios with higher introduction density, which could be due to competition, increased predator pressure, or to a combination of both. Similar trends were observed for Minnow and Trout and Stoneloach, all nodes that received the most energy input from the nodes Diptera, Gammaridae and Trichoptera. Since Gammaridae decreased, at least some of the decrease in the fish nodes could be assigned to competition. Those findings are also consistent with the assumption that *P. parva* is a strong competitor for food resources (Witkowski, 2006; Britton et al., 2010c; Gozlan et al., 2010a). *P. parva* might be the better competitor for energy because of its size, as small individuals have a higher ingestion rate per gram body weight (Peters, 1983) and the flow rates between the nodes are based on the ingestion rate.

The increase in the predators of TopGud also suggested a bottom-up effect. In return, increased top predator body mass could have top-down effects on their prey nodes. The addition of the top predator, Pikeperch, also caused a decrease in Gudgeon and Trout, so some of the decrease could be explained by increased top-down effects. Roach was strongly affected by the introduction of Pikeperch, going extinct at the higher introduction densities. Contrary, Roach abundance increased after TopGud introduction. Roach only forms a small part of the Pike diet and Eel did not prey on Roach at all. This might be the reason why Roach is unaffected by the increased abundance after TopGud introduction. Pikeperch

received 30% of its energy demand from ROACH, resulting in a strong top-down control.

In a comparative study of two ponds with similar community composition of which one was invaded by *P. parva*, no changes in composition or abundance of the fish community were found, although *P. parva* was the numerically dominant fish in the invaded pond (60 m^{-2}; Britton et al., 2010c). Even the highest introduction density for TOPGUD into the food web model was distinctively lower (2 m^{-2}). The present study found a high impact on community composition, which could be explained by the different nature of the habitat (lotic vs. lentic) and fish community composition (Britton et al., 2010c). The ponds were inhabited by five native fish species and top predators were absent. Although a shift in the trophic position of rudd (*Scardinius erythropthalmus*) suggested that it preyed on *P. parva* in the invaded pond, this suggestion would not be supported by gut content analysis. However, *P. parva* was found to depress somatic growth in *R. rutilus*, a finding that contradicts the predicted higher abundance of ROACH in the food web model, although abundance is measured in cal m^{-2} rather than individual growth. When interpreting the different results, it has to be kept in mind that the implementation of TOPGUD diet into the model was intentionally chosen to display high competition with GUDGEON. Contrary to the findings of Britton et al. (2010c), TOPGUD can be assumed to have impacted on other species nodes through competition and also through bottom-up effects on top predators, which in turn elicited top-down effects. In the model, ROACH was hardly affected by those top-down effects and its abundance increased. Therefore, the impacts that a small, highly abundant, competitive species might have on a system with and without top predators is likely to be substantially different.

The introduction of BARBEL had no notable impact on the abundance of other nodes. The food web seemed to be resilient to the addition. BARBEL received its energy input mainly from DIPTERA, with small inputs from other macroinvertebrate nodes. Compared to the diet composition of TOPGUD, BARBEL was a more specialised forager and occupied a different niche, which resulted in no detectable competition for energy with the other nodes. The ingestion rate for the larger-bodied

Barbel was also lower per gram body weight. Although *B. barbus* had been introduced to western and southern England and parts of Italy, negative impacts that are specific to their introduction have not been reported (Bianco and Ketmaier, 2001). The low impact Barbel introduction had on community composition, combined with the absence of reported ecological impacts, suggested that *B. barbus* introductions to chalk streams to enhance the recreational fishery may not result in adverse impacts on stream community structure.

The establishment of the three introduced species nodes followed a different pattern. Pikeperch abundance was in all three cases lower (41−90%) after the model relaxed into the final stable state than introduction abundance, suggesting that only a certain number of individuals could be supported. For TopGud the trend was reversed. Except for the low introduction density, where abundance decreased by $\approx 60\%$, an increase in abundance (30−60%) could be observed. There seemed to be a critical abundance, at which TopGud was able to either out-compete other nodes with a similar diet, or started to have bottom-up effects on top predator nodes. The change in abundance of the nodes after TopGud introduction suggested a combination of both (Figure 5.8). At the low introduction density, TopGud had a positive effect on the abundance of Gudgeon, Bullhead and Stoneloach, while Pike2 abundance decreased. The final stock value of Barbel was in all three cases $\approx 10\%$ less than the introduction density, suggesting that although no major impacts could be detected on community composition, a consistent abundance of Barbel was supported.

From the three model species added to the food web, two elicited changes in the abundance of other nodes and biodiversity: the top predator and the strong competitor. Further investigation is required to ascertain whether the impact caused by TopGud introduction is due to the diet overlap or the high ingestion rate per gram body weight. Presently, the literature is scarce of evidence that ingestion or metabolic rate per gram body weight could be a predicting factor of the invasiveness of a species, although it has been suggested that metabolic rate, which scales with body mass, could be used to predict how the individual affects the dynamics and

structure of populations, communities and ecosystems (metabolic theory of ecology; Brown et al., 2004). Concepts of the metabolic theory of ecology have been applied to ecological networks to estimate interaction strengths between consumers and their resources (Emmerson and Woodward, 2005; Woodward et al., 2005a; Otto et al., 2007; Yvon-Durocher et al., 2008). Stocking up top-predators into the ecosystem can either result in decline of native top-predators because the introduced species replaces them, or increase in predator species richness (Eby et al., 2006). In the present case, PIKEPERCH introduction caused the other top predators to decline, which corroborates observations in waters characterised by elevated turbidity but is contrary to low turbidity waters, where native *E. lucius* is normally the predominant of the two top predators (G.H. Copp, pers. comm.). The energy flow model also shows that it is difficult to predict how the abundance of nodes will be affected, since bottom-up and top-down effects have been seen simultaneously. This has implications for biomanipulation, especially for species rich ecosystems. Direct effects can also be mitigated through indirect effects. For example, although PIKEPERCH preys directly on SALMON, DACE and STONELOACH, the abundance of those three nodes was affected positively after PIKEPERCH introduction.

In real food webs, individuals can change their behaviour (McIntosh and Townsend, 1995), shift their diet (Declerck et al., 2002; Baxter et al., 2004), or be favoured by environmental factors, such as discharge regimes (Marchetti and Moyle, 2001; Thomson et al., 2002; Franssen et al., 2007). Predator impacts on food web structure can also depend on habitat type (Nystrom et al., 2003) and disturbance history (Nystrom and McIntosh, 2003). Further impacts could be caused by habitat modification (e.g. Miller and Crowl, 2006), disease transmission (Blanc, 1997; Gozlan et al., 2005; Gozlan, 2008b), or hybridisation (Gozlan et al., 2010b). The impacts detected by the food web model might be mitigated or amplified by these factors. *P. parva*, for example, has been shown to interfere with the reproduction of native species (Britton et al., 2007) and is also a healthy carrier of the rosette agent *S. destruens* (Gozlan et al., 2005). The food web model does not contain egg or larval species, so *P. parva* could have non-trophic impacts on the abundance of other fish

by being a healthy carrier of a pathogen and additional trophic impacts by preying on larval stages and eggs of fish. Impacts of diet shifts in native species after an introduction have been shown to not only impact on the aquatic system, but also on the surrounding terrestrial community. The introduction of rainbow trout (*Oncorhynchus mykiss*), which mainly feeds on terrestrial prey that falls into streams, to rivers in northern Japan caused native Dolly Varden charr (*Salvelinus malma*) to shift their diet from terrestrial prey to aquatic insects that graze algae (Baxter et al., 2004). This also decreased the abundance of riparian spiders that specialise on emerging adult aquatic insects (Baxter et al., 2004). Changes in stream discharge, or in a wider sense habitat modification caused by water abstraction, favoured non-native species in a Californian regulated stream (Marchetti and Moyle, 2001). The abundance of native species on the other hand, was positively affected by a natural discharge regime, which is defined by higher discharge. These examples illustrate the importance of considering environmental factors and behavioural changes when applying the results from the energy flow model to conservation decisions.

The model was specifically developed for an energy- and species-rich chalk stream. The impacts of introductions in other lotic systems might be different and should, therefore, be tested. Negative and positive effects have also been reported for the same species (Leprieur et al., 2009), which shows that the impact of species might be context dependent. The detected impacts on community structure in the present study are purely explainable by trophic interactions. Although species abundance was influenced by introductions, and a large shift was observed after TopGud introduction, a collapse of the food web was not observed in any of the trials. Additional stressors, such as habitat degradation and environmental change, may therefore play a major role when extinctions are observed (Gurevitch and Padilla, 2004). Future research is needed to determine whether or not the large shift caused by TopGud introduction was caused by the high diet overlap, by the higher ingestion rate due to its smaller body size, or by the combination of both. Although the diet of Barbel was not implemented to simulate competition, it still received its energy from the main prey nodes, but did not elicit detectable changes. Therefore, it is concluded

that ingestion rates could play a major role in determining the impact an introduced species can have on food web structure.

Chapter 6

Impact of rising temperatures on energy flows and distribution within an aquatic food web.

6.1 Introduction

Climate change currently constitutes one of the key global ecological impacts as evidence suggests that the warming process is presently going faster than in the past 1000 years (IPCC, 2007). Climate has always varied temperatures during the earth's history, and this has had a profound influence on the distribution of organisms. Notwithstanding, the current rate at which the environment will change is expected to be too fast for ecosystems to adapt (Mulholland et al., 1997; Malmqvist and Rundle, 2002; Folke et al., 2004; Johnson et al., 2009a; Perkins et al., 2010). The abiotic factors that will directly or indirectly affect aquatic organisms are *i*) water temperature (FSBI, 2007; Johnson et al., 2009a), *ii*) changes in hydrology (indirectly through change in precipitation; Poff et al., 1997; Fruget et al., 2001; Johnson et al., 2009a), and *iii*) CO_2 concentrations (through changes in leaf litter composition; Rier et al., 2002).

During the 20th century, the global mean temperature has risen by 0.6°C, and the

projected increase for the next century ranges from 1.4°C to 5.8°C. Physical variables that are temperature dependent include surface tension, density and viscosity, organic and non-organic chemical reaction rates and solubility of oxygen and other gases (Webb, 1996). Temperature has a large effect on aquatic biotas, which are mostly poikilotherms, as it governs biological processes such as species' distribution (Poff et al., 2002; Sims et al., 2004), and metabolism (Fry, 1971; Coutant, 1987; Regier et al., 1990; Clarke, 1993), with knock-on effects on growth, reproduction, immune responses to diseases (Le Morvan et al., 1998) and ultimately organism behaviour (Kramer et al., 1997; Sims et al., 2006).

This combination of physical and biological changes will determine the extent of shifts in the geographical distribution of organisms. Since enzymatic rates are temperature dependent, and the body temperature of poikilotherms varies according to the surrounding water temperature, fish metabolism is directly linked to water temperature, with direct consequences on food consumption and growth (Brander, 1995; van Dijk et al., 2002), but also foraging behaviourchanges with temperature (Persson, 1986). An increase in thermophilic species in higher latitudes and altitudes has already been observed (Daufresne et al., 2004) and fishes are expected to respond to environmental change by migrating, which might be limited by catchment barriers, to habitats that continue to provide optimum conditions for their metabolism and, ultimately, fitness (Allan et al., 2005). Warmer winters and milder springs favour the recruitment of many cyprinid fishes (Johnson et al., 2009a), whereas cold water species may experience a reduction in habitat (Mulholland et al., 1997). Indeed, a temperature rise is predicted to result in a general increase in system productivity (Benke, 1993; Mulholland et al., 1997). The effects of temperature on different aspects of fish biology can be summarised categorically (Figure 6.1, 6.2) on the complicated, interdependent relationships between mortality and growth, which can respond differently at distinct life-stages, e.g. temperatures that are beneficial for spawning in adult fish can have fatal consequences on egg development (Sandstrom et al., 1997). Behavioural responses to compensate for effects make predictions more difficult. For example, in starving *R. rutilus*, colder waters are preferred in order to

maintain lower metabolic rates (van Dijk et al., 2002).

Similar findings have been reported for macroinvertebrates (Daufresne et al., 2004; Hickling et al., 2006; Johnson et al., 2009a). Macroinvertebrate communitiy composition is used as indicator for water quality, since it is very sensitive to environmental stressors (RIVPACS model; Wright et al., 1984) and temperature influences community composition directly (Durance and Ormerod, 2007).

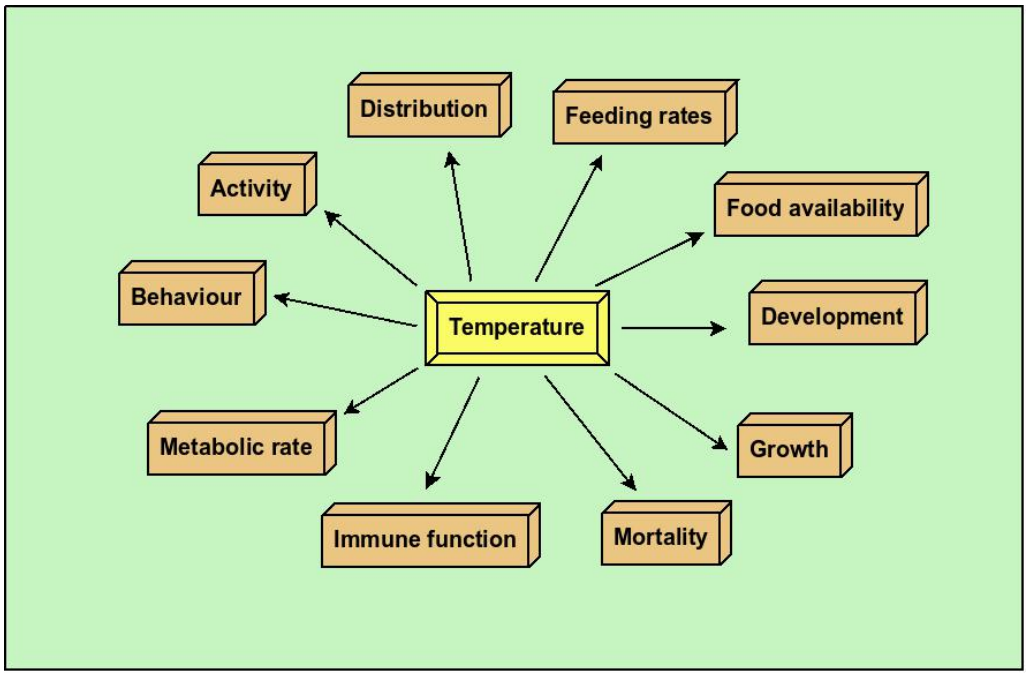


Figure 6.1: Temperature effects on fish biology.

Changes in precipitation (and consequently water flow) are more difficult to predict than changes in temperature, but it is agreed that there will be more extreme weather events (IPCC, 2007). For the UK, an increase in precipitation during the winter month and severe droughts during summer and autumn are expected in the next 50 years (IPCC, 2007). Seasonal precipitation patterns have a direct effect on the discharge regime pattern, which is characterised by the variability in the magnitude, duration, frequency, timing, and rate of change of river discharge (Poff et al., 1997). Discharge varies with region, vegetation, and geology (Poff and Ward, 1989). Although stream discharge is strongly correlated with water temperature (Poff et al., 1997), it can be considered as "master variable", which limits the distribution and abundance of riverine species (Resh et al., 1988; Power et al., 1995). Both, dis-

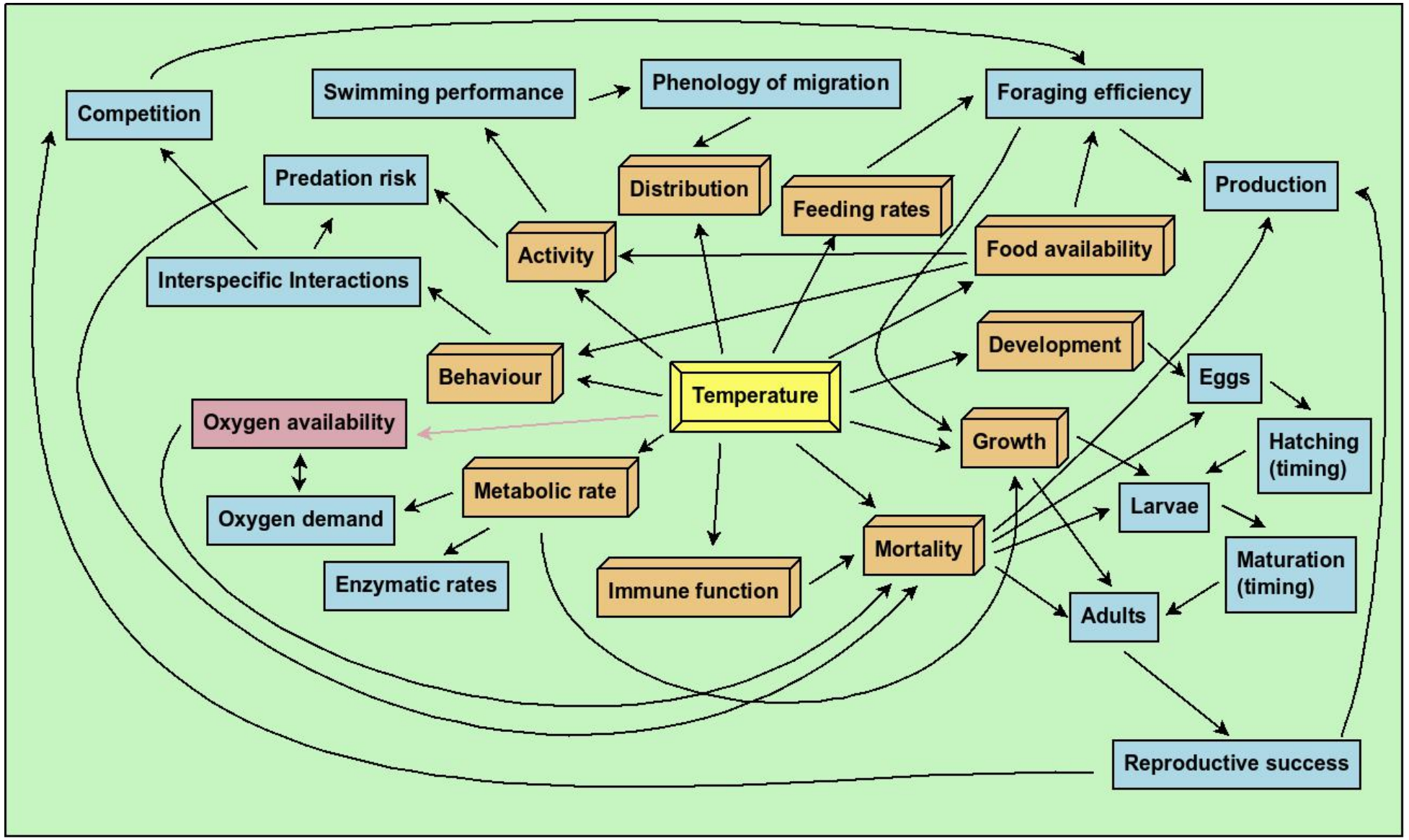


Figure 6.2: Temperature effects on fish biology with interacting factors. Oxygen availability is the second abiotic factor and depends strongly on water temperature.

charge and water temperature have been shown to govern long term dynamics of invertebrate and fish communities (Fruget et al., 2001). The frequency and timing of precipitation seems to be of particular importance. Variable discharge generally maintains high levels of biodiversity (Poff et al., 1997), but changes to the natural discharge regime have been shown to affect biodiversity of fish and certain macroinvertebrates adversely, because habitat diversity declines (Poff and Ward, 1989; Mann and Bass, 1997; Sheldon and Walker, 1997; Baron et al., 2002; Dewson et al., 2007), in particular, a relationship between low discharge and decreases in biodiversity has been demonstrated (Xenopoulos et al., 2005). Additionally, the likelihood of fish being infected by pathogens increases in warm, lentic waters (Johnson et al., 2009a). Some macroinvertebrate families are favoured by drought conditions and and have been found to occur in high densities during periods of low discharge (Dewson et al., 2007). Macroinvertebrate communities have been shown to recover quickly from severe droughts without prolonged impact on species richness (Wright and Symes, 1999). There are still gaps in knowledge on how low discharge affects macroinvertebrate communities, but a shift in community composition towards drought resistant species, at least during low discharge periods, is certain.

The different scenarios of future carbon dioxide release used in climate change forecasts reflect the uncertainty associated with climate change predictions, but global atmospheric carbon dioxide levels are expected to double within the next 50 years (Rier et al., 2002). Elevated carbon dioxide can affect leaf chemistry of C_3 plants through increased C fixation and lead to a proportional decrease in N. Increased C fixation results in less edible detritus input into the river food web, and consequently slower decompostation of terrestrial leaf litter by microbes. In particular, detritus based food webs are expected to be affected where lower availability of C and N at the base of the food web could ultimately decrease production at higher trophic levels (i.e. macroinvertebrates and fish Rier et al., 2002) and change the distribution of feeding links (Hall et al., 2000).

The impacts that climate change might have on ecosystems are correspondingly complex and could affect the physiological and behavioural aspects discussed above.

In Chapter 3, the impact of extinctions, e.g caused by raised temperatures or altered discharge regime, on food web structure was examined. Loss of biodiversity caused by extinctions and range shifts have been predicted (Poff and Ward, 1989; Mann and Bass, 1997; Sheldon and Walker, 1997; Baron et al., 2002) and, in some cases, confirmed (Daufresne et al., 2004; Hickling et al., 2006; Johnson et al., 2009a), but the impact of elevated temperatures on energy flow and distribution has not been investigated. In the previous chapters, the assumption was made that the model system is not energy restricted. Here, the effects of energy restrictions, combined with elevated metabolic rates, on food web structure, which could lead to a decline in production and diversity, are investigated. In an ecosystem where the additional energy demand arising from higher metabolic rates is covered by unrestricted nutrient supply, production should increase.

Aims and objectives

This chapter aims to identify the impact of increased metabolic rates as response to elevated temperatures on biodiversity and community composition. The objectives are:

1. To investigate the influence of elevated metabolic rates without increased energy input on biodiversity and community composition.

2. To determine the effects of elevated metabolic rates with simultaneously increasing additional energy input on biodiversity and community composition.

6.2 Materials and Methods

The energy flow rates of the Baseline Model (Chapter 3) are based on ingestion rates for poikilotherms. The ingestion rates are gradually increased and the new flow rates are calculated. Data from experiments using poikilotherms suggest an increase of between 1.5 and 3.0 times the basic metabolic rate when temperatures increase by 5°C (Peters, 1983). For the modelling trials, the assumption is made that the ingestion rates will increase in the same manner. For each increase, the model is run twice. (1) without an increase in energy input (Community IDs 1–4: see Table 6.1) to simulate energy restriction, and (2) with an additional energy input from the environment (Community IDs 5–8) matching the increased ingestion rates (Table 6.1). The resulting communities are compared in terms of changes in biodiversity (Shannon index), the extent of extinctions, changes in total energy and distance between the communities (Bray-Curtis measure). In this context, a species is considered as extinct if its abundance decreases below 5% of its abundance in the Baseline Model.

Table 6.1: Increase in ingestion rates, which equivalents an increase in temperature by 5°C, and additional energy input of each trial.

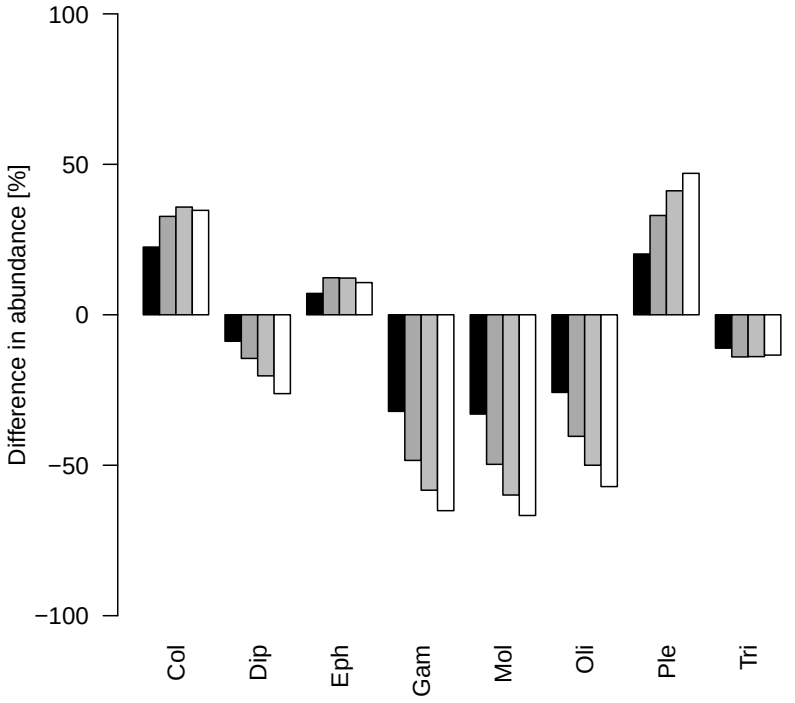
Community ID	Increase in ingestion rate	Increase in additional energy input
1	1.5×	none
2	2.0×	none
3	2.5×	none
4	3.0×	none
5	1.5×	1.5×
6	2.0×	2.0×
7	2.5×	2.5×
8	3.0×	3.0×

6.3 Results

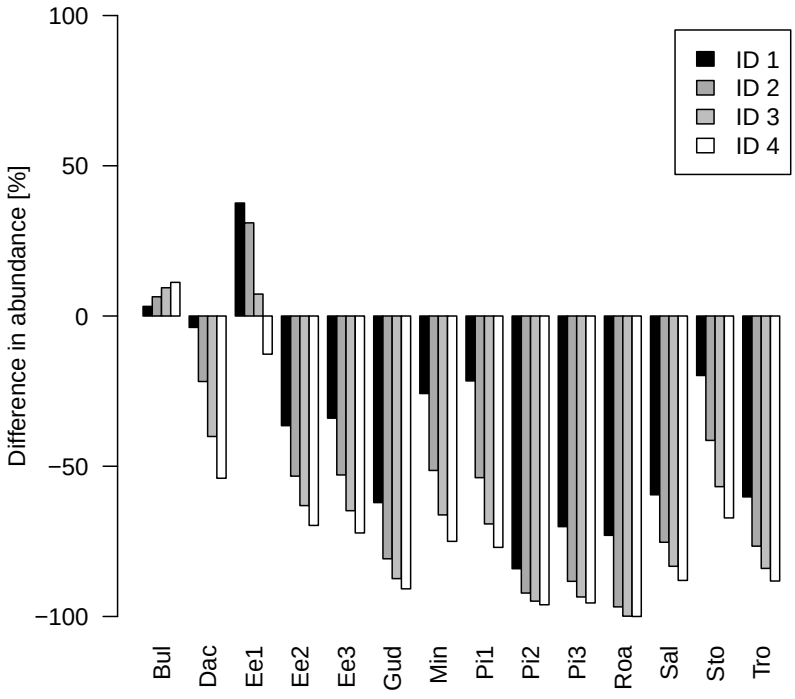
The communities that received an increased additional energy input (IDs 5–8) showed no change in species diversity, whereas nutrient-restricted communities showed a decrease in species diversity (Table 6.2). In the restricted communities, almost all species nodes became less abundant with increasing metabolic rates. The abundance of nodes, such as Gudgeon, Pike2, Pike3, Roach, Salmon and Trout decreased over 75% compared to the Baseline Model (Figure 6.3), with an increase of Coleoptera and Plecoptera. However, both nodes had very low abundances in the Baseline Model, so that the absolute abundance values hardly changed. Extinctions occurred in six cases within the energy restricted communities. In Community 2, Roach went extinct, in community 3, Roach and Pike2, and in Community 4, Roach, Pike2 and Pike3. In communities that received additional energy input, no extinctions occurred and abundances hardly changed (Figure 6.4). MDS analysis supports the findings that the energy restricted communities were more dissimilar to the Baseline Model (Figure 6.5). With increasing ingestion rates, communities 1–4 shifted further away, whereas communities 5–8 remained close to the Baseline Model. The total energy of the system was reduced by 40 to 74% of the energy stored in the Baseline Model in the energy restricted communities, whereas only a small positive increase in total energy could be observed when energy was not restricted (Table 6.3). Fish abundance in communities 1–4 decrease proportionally more than macroinvertebrate abundance.

Table 6.2: Shannon-Diversity Index *H'* and true diversity (exp(*H'*)) for the communities after increasing ingestion rates.

Community ID	Shannon index *H'*	True diversity
3	2.36	10.6
4	2.37	10.7
2	2.39	10.9
1	2.48	11.9
7	2.54	12.7
8	2.54	12.7
6	2.54	12.7
5	2.54	12.7
Baseline Model	2.54	12.7

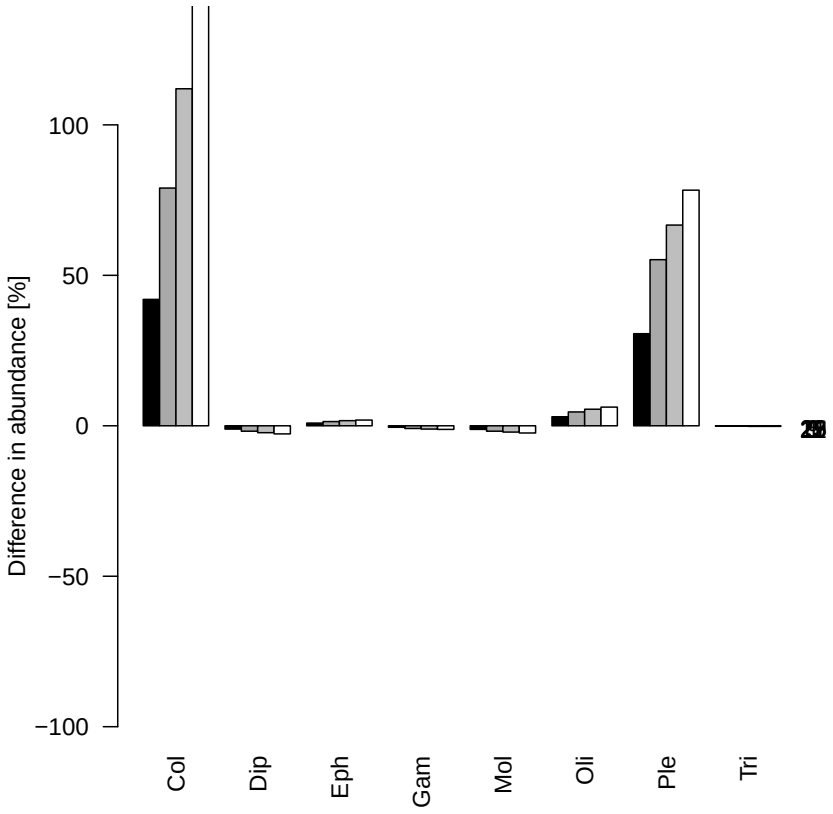


(a)



(b)

Figure 6.3: Impact of increased ingestion rates with unchanged energy input on the abundance of macroinvertebrate nodes (a) and fish nodes (b) relative to the final values of the Baseline model. For abbreviations see Appendix Table A.3.



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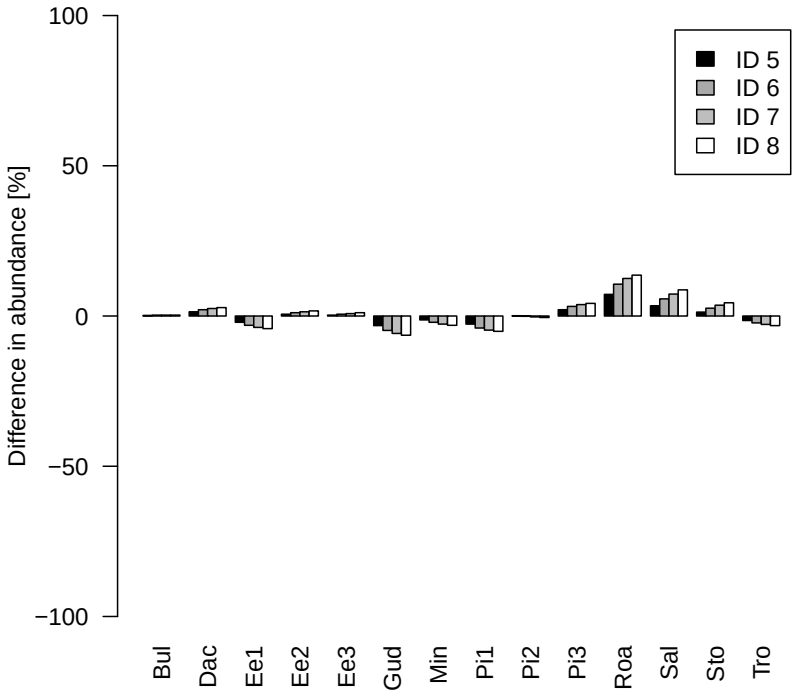

(b)

Figure 6.4: Impact of increased ingestion rates with increased energy input on the abundance of macroinvertebrate nodes (a) and fish nodes (b) relative to the final values of the Baseline model. For abbreviations see Appendix Table A.3.

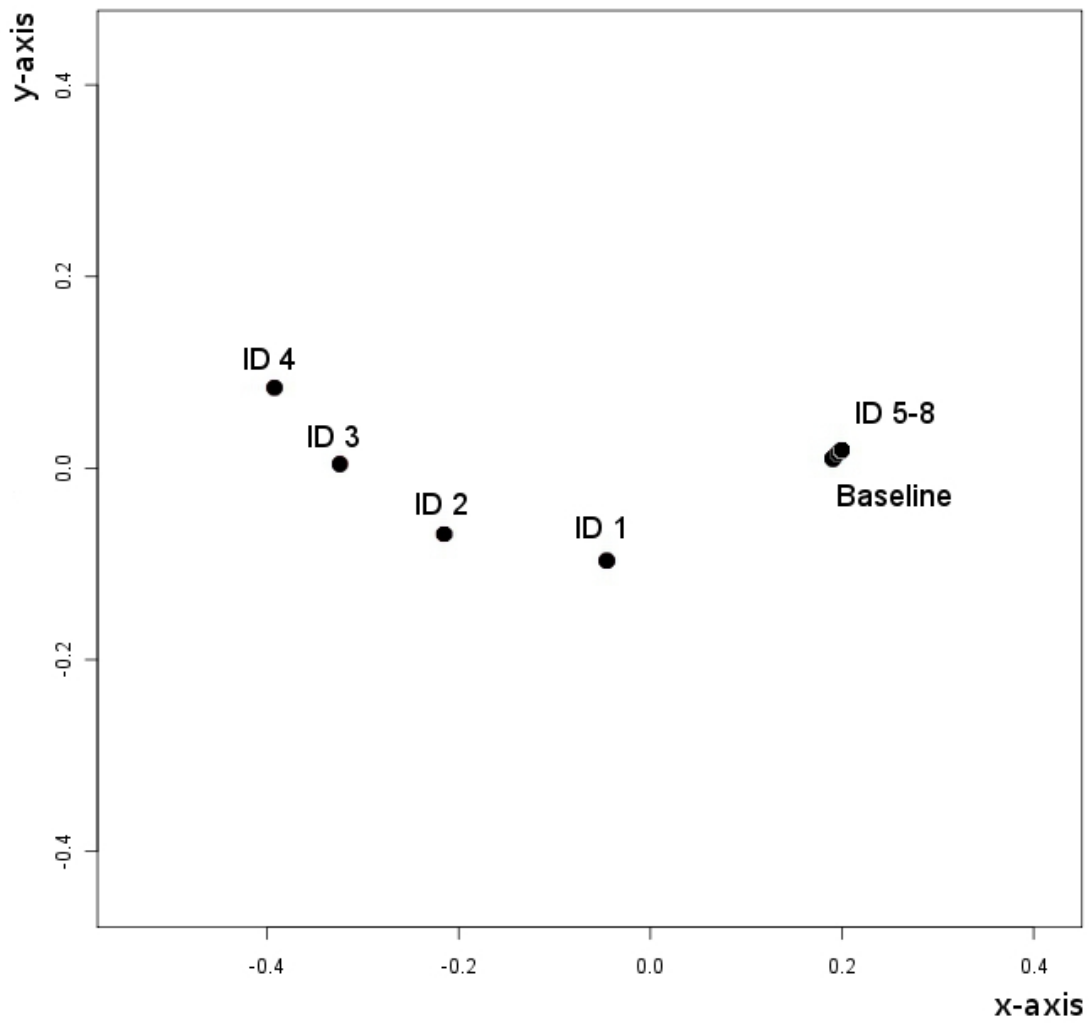

Figure 6.5: MDS ordination for the communities after increasing the ingestion rates. The axis are dimensions. Stress: 0.00%.

Table 6.3: Difference between total energy of modelling trials 1–8 and the Baseline Model.

Community ID	Difference between observed and expected total energy [cal m^{-2}]	Difference between observed and expected total energy [%]		
		All nodes	Fish nodes	Invertebrate nodes
4	-22613	-74.0	-55.9	-18.1
3	-20717	-67.8	-51.6	-16.2
2	-17762	-58.1	-55.9	-13.4
1	-12434	-40.7	-31.9	-8.8
5	318	1.0	1.1	-0.1
6	484	1.6	1.7	-0.1
7	586	1.9	2.0	-0.1
8	655	2.1	2.3	-0.1

6.4 Discussion

The effects of climate change are likely to influence numerous aspects of fish physiology or ecology. This chapter investigated the impact of elevated ingestion rates as a result of increased temperatures on food web structure. The impact of elevated ingestion rates were catastrophic when energy input into the food web was not raised to match the higher energy consumption. An overall decrease in species abundance, biodiversity and total energy was subsequently observed. When the higher energy expenditure was matched with higher energy inputs, biodiversity and community composition remained similar to the Baseline Model, with slightly increased values for total energy (production).

The Millstream food web is strongly dependent on detritus as a baseline energy source (Westlake et al., 1972; Dawson, 1976; Hynes, 1983); although primary production is high, living macrophytes are considered to play a small role as energy sources for secondary production, since few macroinvertebrates feed on them (Newman, 1991; Pinder, 1992). Reduced decomposition rates caused by changed nutrient composition of detritus, as a consequence of increased atmospheric CO_2 concentration, might pose a restriction on energy input at the base of the food web (Rier et al., 2002). The response of the model system to increased metabolic rates in the two scenarios highlights the importance of sufficient energy supply. This is only one aspect of possible responses to climate change, as organisms can show behavioural adaptions to counteract the found effects, or species might be replaced by species that belong to the same functional group, but have distinct temperature requirements or are better adapted to the changes in leaf litter composition. For example, Hall et al. (2000) demonstrated that link distributions and intensities changed in a leaf litter limitated stream and wood became a more important resource. Additionally, food chain length might decrease with lower energy inputs from detritus (Jenkins et al., 1992).

Behavioural responses that have been shown for fish include migration and changed activity patterns, and they could counteract the impact of elevated temperatures

by saving energy expenditure. For example, starved *R. rutilus* showed a preference for colder waters during night while resting and was less active than *R. rutilus* held under control conditions (van Dijk et al., 2002). When sufficient food is available, warmer temperatures can have positive effects on growth (Garner et al., 1998). *P. phoxinus* forage in the main channel of the River Frome, where food is abundant, but prefer to rest in warmer shallow habitats (although low food availability; Garner et al., 1998). *P. phoxinus* in these warmer habitats showed higher growth rates than fish that remained in the slightly colder main channel. Dependent on food availability, these two cyprinid species showed different strategies to maximise growth. In brook trout (*Salvelinus fontinalis*), higher growth rates were associated with higher temperatures in winter and spring, but lower temperatures in summer and autumn (Xu et al., 2010).

Prolonged warm temperatures in combination with drought conditions might reduce retreat areas that offer lower temperatures and fish density in those refugia might increase. Fish retreat both upstream and downstream into refugia during times of drought and fish assemblages change accordingly (Davey and Kelly, 2007). Migration and increased mortality due to temperature rise could act as an additional stressors, with further negative impacts on biodiversity. As demonstrated in Chapter 4, loss of single species did not have catastrophic consequences on the stability and species composition of the food web, but migration would create, at least temporally, new assemblages that potentially have different properties than the studied food web. In the extreme case of a drought, fish might be confined to pools, in which predatory fish can exert strong predation pressure (Power et al., 1995). Increasing temperatures and lowering oxygen levels in these pools can pose additional threats to fish (Lake, 2003). Considering that temperature operates at a relatively large scale within a basin, changes in thermal conditions can explain replacement of one fish assemblage by another (Rahel and Hubert, 1991). Since fish species have distinct requirements to temperature, especially regarding reproduction, responses to changes in temperature will differ. Pont et al. (2005) predicted the occurrence of fish species depending on six environmental variables (i.e. river slope, river width, upstream drainage area,

mean annual and mean range air temperature and basin unit). For six species (*S. trutta*, *C. gobio*, bleak (*Alburnus alburnus*), *R. rutilus*, *G. gobio* and chub (*Squalius cephalus*), mean annual temperature was of primary importance, suggesting that temperature might be a key variable in explaining their geographical range (Pont et al., 2005). Species that did not show a significant response to mean annual temperature were known to spawn early in the year (*B. barbus*, *L. leuciscus* and *B. barbatula*). Reproductive and recruitment success under altered thermal conditions is also not included in the food web model, but would be an important factor to consider for future predictions.

Growth and development of macroinvertebrates are also temperature dependent. For particular species, growth, development and consequently production will be maximised at a certain temperature or temperature range; either side of that optimal temperature production is reduced (Reynolds and Benke, 2005). Accordingly, production and biomass patterns can vary annually for different species of the same taxa (e.g. trichoptera; Benke and Wallace, 1997). Although temperature seems to be a significant factor in determining growth (Benke et al., 1992), food quality and availability also plays a role (Benke and Wallace, 1997; Benke, 1998). Thus temperature effects should be assessed in the context of energy availability. Furthermore, in a nine year study of the macroinvertebrate assemblage of a chalk stream, Wright and Symes (1999) found that the macroinvertebrate assemblage shifted according to drought years and those of high discharge. For example, chironomidae (diptera) were more abundant in drought years, whereas simuliidae (diptera) and baetidae (ephemeroptera) were generally more abundant during years with high discharge. Overall, family richness hardly varied, and recovery after drought years was rapid. Although environmental conditions favoured macroinvertebrate families differently, overall macroinvertebrate abundance remained similar. In that study, drought years were followed by years of higher discharge, giving the macroinvertebrate community the opportunity to recover. If drought years become more frequent due to climate change, then species that are favoured by higher discharge, might not get the opportunity to recover. Removal of Ephemeroptera, which contains families that

were less abundant during low discharge, was followed by secondary extinction of ROACH (see Chapter_4). Low abundance of favoured prey item might therefore have cascading effects on predator populations. The effects of prolonged droughts on macroinvertebrate community can have negative effects on diversity and overall abundance. A four year study of the macroinvertebrate community in the River Little Stour (a chalk stream) showed that macroinvertebrate diversity and abundance were low after a drought period between 1988–1992 (Wood and Petts, 1999). The study was started in the last year of the drought period, 1992 and lasted until 1995, so macroinvertebrate community composition was not available for the time before and during the drought period. Although diversity and abundance was low in 1992, the macroinvertebrate community recovered in the following years with higher discharge, but recovery lasted longer compared to the shorter drought periods monitored by (Wright and Symes, 1999). As a consequence of climate change, droughts are not the only factor to consider. Floods, which are predicted to occur more frequently, could also have potential impacts on macroinvertebrate communities, but it was shown that high discharge years had no detrimental consequences on macroinvertebrate assemblage in four perennial chalk stream sites (Wright et al., 2004).

In summary, the nutrient restricted food web became less diverse and might therefore be less resilient to additional perturbations. The loss of a particular species group can be followed by secondary extinctions. Fish nodes were, in general, more affected, suggesting strong bottom-up effects. The results from the present study stress the importance of energy availability for ecosystem stability, and important ecosystem services, such as fish production. Perturbations such as riparian clearing could lead to higher water temperatures and less allochthonous input (Allan, 2004), but also water abstraction can amplify effects of droughts. Macroinvertebrate communities seem to be able to recover quickly after short droughts, but impacts of prolonged droughts seem to be more severe (Wood and Petts, 1999; Wright and Symes, 1999; Wright et al., 2001, 2004). Recovery of communities (macroinvertebrates and fish) depends on the availability of refugia (Lake, 2003), therefore, conservation efforts

should ensure a heterogeneous habitat that offers such refugia, from where species can recolonise.

Chapter 7

General Conclusion

7.1 Summary of the principal results

A dynamic food web model was successfully developed for the study site and provided a Baseline Model that resembled the observed food web sufficiently enough to enable to assess responses to environmental perturbations and species introductions to be identified through impacts on community composition. Two principal procedures in developing the food web model were likely to have had stabilising effects on the food web model: *i*) aggregation of invertebrate species; and *ii*) additional energy inputs from the environment. Aggregation of macroinvertebrate species was necessary due to the available empirical data on trophic links and diets of invertebrates at species level. The additional energy input achieved a steady state of the Baseline Model that allowed for further manipulation and the stabilising effect of these inputs was shown (Chapter 3), since without those inputs extinctions were high. However, due to species aggregation on the macroinvertebrate level, the nodes represented 'super-organisms' and stabilising effects that potentially arise from: *i*) heterogeneity (e.g. different body size and diet) of the assemblages that are summarised in a single node; and *ii*) food web structures in which sub-networks are connected by larger and also more mobile species were not accounted for (Winemiller and Jepsen, 1998; Woodward et al., 2005a; Chapter 2). Additionally, energy transfer could have

been attenuated on the macroinvertebrate level, since all predatory macroinvertebrate nodes preyed on each other and only 10% of the energy, which is transferred from the prey to the predator node is available for the following predator-prey interaction. The stability of the Baseline Model has consequences for the subsequent manipulations of the model. Potentially, the food web model could be more stable than the natural food web, thus, impacts of manipulations on community structure and biodiversity might not be detected or be reduced.

Although impacts on community composition and biodiversity were observed after species removals, the food web could be characterised as resilient to this perturbation. Keystone species as such were not identified, but key trophic positions. Notably, the largest impacts were recorded when important food sources or species of high trophic status were removed, suggesting a certain degree of redundancy for the nodes in intermediate positions, which could also add resilience (Naeem, 1998; Elmqvist et al., 2003, Chapter 2). Food web model properties that could have positively influenced resilience were identified as species aggregation and stabilising effects of additional energy inputs. Ecological properties that could influence resilience positively could also be associated with the high variability of the natural communities, which served as reference points. This high natural variability means that large changes in the abundance of a few nodes as response to node removals is not detected as system shift. For example, some of the removals had large impacts on the abundance of other nodes (e.g. Eel removal caused an increase of >1000% in Bullhead, and Ephemeroptera removal caused Roach to go extinct, Appendix, Figures D.4–D.8), notwithstanding, a system shift was not detected when the Bray-Curtis distances to the natural community were assessed. Furthermore, changes in biodiversity were observed. However, they could not be linked to secondary production as the investigated ecosystem service.

Three model species with different characteristics were introduced into the food web model: a top predator (Pikeperch), and two species of intermediate trophic position (Barbel and TopGud) of which TopGud was introduced with a similar diet composition as Gudgeon to simulate competition. There were no detectable im-

pacts after Barbel introduction, Pikeperch caused extinctions after introduction and the largest decline in diversity at higher introduction densities, whereas Topgud caused the largest community shifts at higher introduction densities. Barbel introduction resulted in slightly increased biodiversity and possibly redundancy, which might add to the resilience of the system, although this was not tested. Introduction densities for Pikeperch were not supported by the food web and so their abundance declined. Introduction of Pikeperch had both negative and positive effects on the abundance of other nodes, but the species has not been found to negatively impact fish populations in empirical studies (Smith et al., 1998) and accompanying declines in prey fishes were attributed to other factors. Nonetheless, the introduction of a top predator caused large declines in diversity and so suggests that they have the potential to reduce prey fish abundance within a food web context. However, changes in community composition, as measured by the Bray-Curtis distance, were less notable. TopGud introduction at higher densities caused large community changes and a slight increase in diversity. TopGud was the only introduction that increased in abundance, at least at higher introduction densities, and it was hypothesised that TopGud is a successful competitor because of its small size and associated high ingestion rate.

Impacts on food web structure as a result of increased ingestion rates could only be observed when energy input was restricted, but then the effect was significant, causing most species to go extinct. Similar to the procedure applied in Chapter 3, additional energy inputs stabilised the food web, and no extinctions occurred.

7.2 Comparison of results versus empirical and modelling studies

The aggregation of invertebrate species might have contributed to a certain degree to the stability of the food web model. It is common practise to aggregate species and to estimate predation links where data is not available (Baird et al., 2009),

but this procedure has not been without criticism. Cohen et al. (1993) point out that even when species are aggregated into trophic species with the same prey and predators, differences in the strengths of connections are obliterated. This might be important for some ecosystems, but for freshwater systems it is unlikely to have a significant effect. For example, intraspecific and seasonal variation in fish diets is possibly higher than variation in interaction strengths of species that share identical prey and predators (Maitland, 1965; Mann and Orr, 1969; Mann, 1971) and prey selection in freshwater systems is more influenced by body size than by taxonomic affiliation (Berlow et al., 2004; Emmerson and Woodward, 2005; Woodward et al., 2005a; Petchey et al., 2008; Ings et al., 2009).

However, it has been suggested that stabilising effects also emerge from sub-networks, which are interconnected by larger, more mobile species (Winemiller and Jepsen, 1998; Woodward et al., 2005b). Earlier, more detailed versions of the Millstream food web, particularly in regard to the representation of macroinvertebrate species proved to be unsuitable for further manipulation, because they did not relax into a suitable stable state. The establishment of realistic sub-networks that potentially could have stabilised the food web without additional energy inputs was not achieved, which was attributed to insufficient data on feeding links for macroinvertebrates. Gut content analysis for the establishment of better resolved macroinvertebrate predation links involves the identification of small prey items that may be partially digested (e.g. Hall et al., 2000). Often macroinvertebrate guts are empty (Woodward et al., 2005b) and links to rare species are poorly defined due to small sampling sizes (Hall et al., 2000). However, the aggregation of macroinvertebrate nodes alone did not lead to a stable food web in this study. Here, stability was mainly achieved through additional energy inputs (O'Neill, 1976).

Although keystone species were not identified, as no defined system shifts could be observed, some species had more influence on community composition than others. The removal and the addition of top predators caused notable changes in community composition and species diversity. The removal of both top predator nodes, Eel and Pike resulted in a relative increase compared to the expected diversity (Table 4.1),

whereas the introduction of PIKEPERCH decreased species diversity (Table 5.4). The changes in community composition caused by top predator introduction were not as distinct as the ones caused by top predator removals, which were identified as the most dissimilar communities compared to the Baseline Model (Figure 4.1 and 5.5). Species of high trophic status have been shown to exert large effects on community structure and diversity (Paine, 1969b; Power, 1990; Eby et al., 2006) with trophic cascades being most pronounced in lentic freshwater ecosystems (Shurin et al., 2002; *cf.* Chapter 2.3.3). Predator presence does not necessarily trigger a trophic cascade, despite eliciting a negative response of prey, for example, *S. trutta* was found to impact large invertebrate prey without inducing a trophic cascade on periphyton (Meissner and Muotka, 2006). The food web model successfully predicts similar top-down impacts, as the removal of PIKE released predation pressure on GUDGEON and the removal of EEL released predation pressure on BULLHEAD, but no knock-on effects on macroinvertebrates that BULLHEAD and GUDGEON prey upon were observed. Weaker trophic cascades in lotic systems might be due to higher prey exchange rates (migration; Cooper et al., 1990), which are represented by the additional energy input in this study.

This finding is also consistent with the bottom-up : top-down theory (McQueen et al., 1986), which predicts that top-down effects should be strongest at the top of the food web and weaken towards the bottom, whereas bottom-up effects should be strongest at the bottom of the food web and weaken towards the top (McQueen et al., 1989). In comparison, hypotheses that suggest that changes in top predator biomass will cascade down to the food web (e.g. biomanipulation concept; Shapiro et al., 1975; 1982; Shapiro, 1980; cascading trophic interaction theory; Carpenter et al., 1985) could not be verified. Although an attenuation of top-down effects has been found, the above theories were developed for pelagic freshwater ecosystems, which are less open to migration and energy fluxes than lotic systems.

Besides these top-down effects, impacts on food web structure were also observed after the removal of the four most important prey items. Two removals caused a secondary extinction and the other two removals caused declines in fish abundances, al-

though predator consumption rates on the remaining prey nodes were raised. These four removal communities could also be found further away from the Baseline Model in the MDS graph (Figure 4.1). However, they were not only dissimilar to the Baseline Model, but also to each other, which suggests that the loss of distinct diet compositions, ingestion rates and predation pressure has different effects on community structure, highlighting the importance of trophic relationships. In general, there are two main outcomes that could be expected from prey removal: *i*) predator abundance decreases (bottom-up control); and *ii*) abundance of remaining prey decreases (top down control). Here, both phenomena were observed simultaneously (Appendix, Figure D.5). The strength of bottom-up and top-down processes and the resulting consequences for food web structure could therefore be strongly context dependent (Power, 1992). In this case, the only traits incorporated into the model were trophic, i.e. consumer diet, predation pressure a consumer is experiencing and ingestion rates. Additionally, the strength of bottom-up and top-down influences in real ecosystems might change dependent on species richness (Wojdak, 2005), temperature (Hoekman, 2010), availability of cover (Crowder and Cooper, 1982; Carpenter and Lodge, 1986), predator-prey size ratios and predator efficiency (DeBruyn et al., 2004).

Climate change has the potential to result in a range of consequences for the food web structure of freshwater ecosystems. Rising temperatures increase productivity, but elevated CO_2 concentrations may adversely affect energy supply from detritus with further consequences on food web structure, such as number of trophic levels (Jenkins et al., 1992), link intensity and species composition (Hall et al., 2000). Prolonged droughts have also been shown to adversely impact on invertebrate species abundance and change community composition (Bond et al., 2008). If macroinvertebrate assemblages lack important prey items as a result of droughts, then a severe decline in fish abundance could follow, with extinctions most likely at the top of the food web (Petchey et al., 1999; Raffaelli, 2004; Perkins et al., 2010). As a result, smaller fish species, such as *C. gobio* or *P. phoxinus* could potentially benefit, when released from predator pressure. Temperature has direct effects on reproductive

success, for example, young-of-the-year pumpkinseed (*Lepomis gibbosus*) grow fast in warmer waters and reach maturity early (Dembski et al., 2006). However, high mortalities were observed after the first brood in these fish. In general, poikilotherms mature earlier and at a smaller body size in warmed waters (Atkinson, 1994). Freshwater systems have been shown to generally become more productive with higher water temperatures (Benke, 1993; Mulholland et al., 1997), but dependent on the species' temperature range, impacts on distribution differ. For example, Daufresne et al. (2004) observed an increase in *B. barbus* and a decrease in *L. leuciscus* as a result of climate warming. Furthermore, species range shifts could lead to loss of salmonid species. The loss of salmonid species did not have major impacts on food web structure, but removal of the node that represents *L. leuciscus* caused differences in community composition and a decrease in diversity.

The overall decrease in diversity and complexity can facilitate invasions (Stachowicz et al., 1999; Chapin et al., 2000; Knowlton, 2001). Once an ecosystem has been invaded, further invasion might be facilitated (Vitousek et al., 1987). Fast reproducing and small bodied species can be highly invasive (Gozlan et al., 2010a), which was also predicted in the present study (Chapter 5). However, they can also respond more vulnerable or opportunistic to changing environmental conditions (DeAngelis et al., 2005). This makes it difficult to predict the success of a small competitor in a dynamic environment that might experience more severe weather events in the future. Although the establishment of the small competitor was predicted, the findings are solely on the basis of trophic interactions, excluding environmental dynamics. Potentially, small bodied species are more successful to establish in less dynamic freshwater systems, such as lakes or ponds (DeAngelis et al., 2005). On the other hand, it was found that worldwide the introduction (and subsequent establishment) of economically interesting, larger bodied species can shift the size-distribution in river food webs (Blanchet et al., 2010). Here, the introduction of a top predator had some impact on food web structure, but stronger impacts of top predator introduction have been found for pelagic systems, e.g. the introduction of *E. lucius* replaced native Arctic char (*Salvelinus alpinus*) in a subarctic lake (Bystrom et al.,

2007). Potentially, a shift towards larger-bodied species is more likely in dynamic lotic systems, as introduced larger-bodied species are more likely to co-exist than in pelagic systems, which was supported by the findings after the introduction of a larger-bodied species at intermediate trophic level of the food web model. Additionally, a shift of body size ratios can also influence the strength of trophic cascades (cf. Chapter 2).

To assess impacts on ecosystem function, the change in secondary production was measured, which generally decreased after the removal of macroinvertebrate nodes and increased after the removal of fish nodes, but could not be linked to species diversity. Diversity has been shown to impact on ecosystem services (Walker et al., 1999; Loreau and Hector, 2001), but few species are actually needed to maintain normal ecosystem function (Schwartz et al., 2000), particularly when only one process (i.e. trophic) is assessed (Reiss et al., 2009). Presently, impacts on secondary production was the only ecosystem function that was assessed with the food web model, but it would be desirable to assess impacts on other ecosystem functions, such as primary production (e.g. Power, 1990) or detritus processing rates (Woodward et al., 2008) in future experiments. Winkelmann et al. (2011) found in large scale removal experiments that fish predators had more impact on macroinvertebrate community composition than on secondary production. Although fish removals caused an increase in secondary production in the present study, changes in macroinvertebrate community composition could not be assessed precisely due to the highly aggregated macroinvertebrate nodes. But interestingly, removals (of fish and macroinvertebrate nodes) caused higher relative changes in fish than in macroinvertebrate abundances (Appendix D.2). Macroinvertebrate abundances would increase or decrease by maximum 50% in a few cases, whereas fish abundances would change comparably more, suggesting that, generally, fish community composition was affected more by removals. It is not clear what caused this effect, but macroinvertebrate aggregation is likely to hide more dramatic changes in macroinvertebrate community composition. However, in the experimental study of Winkelmann et al. (2011) all fish were removed, so it could not be compared if impacts on the fish community were possibly

stronger than on macroinvertebrate community composition.

7.3 Implications for chalk stream management

Although the nodes in the food web represented species or families, model results concerning the importance of a species or family have to be interpreted carefully in regard to river management. Presently, only important trophic positions have been identified with this approach, as no keystone species have been found. The approach taken was a systems approach and the results of the removal experiments suggest that this approach should be applied to river management rather than protecting single species.

Chalk stream environments are characterised by high species diversity and production (*cf.* Chapter 3.2.1). They are groundwater fed, so low precipitation during the winter month can have impact on groundwater levels, which can lead to reduced discharge during summer droughts (Wood and Petts, 1999), but if aquifiers are full, summer droughts will be less severe. Additionally, groundwater-fed streams have a relatively stable temperature regime, as they are less dependent on ambient air temperature. Creed (2006) proposed a conceptual model, which suggests that predation might be more important for shaping community structure in ecosystems with benign disturbance regimes, such as groundwater fed streams. Here, we found that the Millstream food web model is relatively stable against a range of disturbances, although still affected by changes in predation pressure at the top of the food web.

Predicted extreme weather events (higher precipitation in winter and prolonged droughts in summer) might have less impact on groundwater fed streams, as aquifiers fill up in winter, which might result in less severe effects of droughts in summer. However, increased demand for freshwater and associated water abstraction could still result in low flows with consequences on macroinvertebrate community composition. In Chapter 4, I showed that the loss of important invertebrate prey items can lead to secondary extinctions in fishes. Although macroinvertebrate assemblages

have been shown to recover quickly after droughts (Wood and Petts, 1999; Wright and Symes, 1999), increased water abstraction could add negative effects and should therefore be managed carefully.

Communities that are energy restricted have been shown to be less stable (*cf.* Chapter 6), in particular with warming temperatures. This has implications for river bank and land use management. Tree cover and vegetation can add valuable energy inputs (detritus) into the river. Additionally, tree cover provides shadow against direct sunlight and reduce increases water temperature (Allan, 2004). Furthermore, the stabilising effect of additional energy input, which could be interpreted as migration, has implications for damming or other obstructions for migration. Negative impacts of obstructions on physical, chemical, and biological characteristics of rivers has already been pointed out (Poff et al., 1997; Poff and Hart, 2002), so the findings of this study support the necessity of keeping migration pathways open.

Although no correlation between species diversity and secondary production as a measure of ecosystem function was found in this study, empirical studies suggest that biodiversity is crucial to maintain ecosystem function after disturbances (Downing and Leibold, 2010). For example, a reduction in detrivore diversity can result in reduced decompostation rates (Srivastava et al., 2009). Furthermore, species poor stream communities break down leaf litter more slowly than species rich communities (Benstead et al., 2009). Lecerf and Richardson (2010) list measures of ecosystem function directly relevant to streams. Additionally to measures of energy and material distribution and measures of energy fluxes and material processing, ecosystem function can be measured by the ability to remain stable against disturbances, such as invasion or climate change. With the findings of this study, chalk streams that are comparatively undisturbed, which was assumed for the study site, proved relatively resilient to various disturbances. Healthy stream ecosystems should therefore be capable of maintaining their function in the background of environmental change, if anthropogenic stresses are managed carefully. More impacted rivers should contain healthy, well managed sections from which migration into the impacted sections is possible. This could potentially add to stabilising the impacted sections and ensur-

ing the supply of ecosystem services.

The results of the current study suggest that chalk stream conservation should focus on maintaining or restoring structures that promote a diverse community, which is resilient to disturbances, rather than focusing on the conservation of single species. Heterogeneous, natural habitats offer refugia for biota, which is important for rapid recolonisation after disturbances that cause species loss, such as droughts or high discharge events. Riparian vegetation can mitigate the influence of direct sunlight and provides valuable energy inputs. The results of the current study also suggest that probably one of the most important structural necessities is a connected river, so species migration is possible, as energy inputs had stabilising influence on the food web. Specifically, streams and river communities have to persist in a dynamic environment that is characterised by change a lot more than e.g. a mature forest. A healthy ecosystem is also more resilient to invasions, which is important, as removal programs of undesirable invasive species are difficult and expensive. Access to heterogeneous habitat is particularly important for fish, as they will take different trophic positions during ontogeny, therefore adding redundancy on several levels, and their habitat requirements can differ greatly between juveniles and adults. Rather than species conservation, it might be more useful to identify 'Keystone structures' that provide the system with the opportunity to maintain resilience in regard to the raised points.

7.4 Future work and predictive approaches

Like all models, the Millstream food web model is a compromise of simplicity and adding enough detail to reflect mechanisms that work in a natural environment. It was discussed how simplifications could reduce the predictive value of the results. However, the model clearly displays patterns that have been found in experiments.

The results also raise further questions that could be addressed in future experiments. The influence of species aggregation and additional energy inputs on im-

pacts caused by species removals and introductions on food web stability should be explored further. In particular, because species aggregation is broad and necessary practise and, in this case, energy flows at the lower levels of the food web were highly simplified. Information about the impacts of species aggregation would not only be beneficial in planning modelling approaches, but also in planning data collection for characterising food webs. This could be achieved by sub-dividing macroinvertebrate compartments further into functional groups rather than solely taxonomic classification. Additionally, nodes that represent primary production and detritus should be incorporated. With this modification the influence of functional diversity on ecosystem function, such as production, could be further investigated. This knowledge would be of particular interest with predicted reductions in macroinvertebrate diversity caused by droughts.

Secondly, additional energy input was proven to have a stabilising effect. However, it was hypothesised that the interconnection of macroinvertebrate nodes caused more energy loss than would be observed in a natural system, since all predatory nodes fed on all other macroinvertebrate nodes. This structure causes energy to cycle at this level and energy is lost because only 10% remains available to the next consumers. Theoretically, less aggregated macroinvertebrate nodes that form smaller sub-networks connected by larger predators, such as fish, could reduce the amount of additional energy that is necessary to produce a Baseline Model.

Mean values from empirical data served as basis for the Baseline Model. The predictions were made from one set of model runs, which is a limitation in the predictive power of the model. Firstly, the influence of different starting values should be explored. Model runs were already performed with differing fish community composition (i.e. starting values were acquired from the seasonal abundances of the empirical data) and species were removed from these models (see Appendix D.1 for examples). The same starting values for macroinvertebrate nodes and additional energy inputs values were used, which all resulted in acceptable baseline models (i.e. the model relaxed into a steady state that resembled the starting values closely). So far these results support that the removal of important prey nodes and top predators

causes larger dissimilarities to the Baseline Model. Secondly, the influence of body size on food web dynamics could be explored further, by changing ingestion rates accordingly.

Concerning the introduction of species, ingestion rates could potentially have influence on the success of establishment and spread of a species. In the present study, TopGud was the only introduced node that increased in abundance at high introduction densities, which could be interpreted as successful establishment. It has been suggested that metabolic rates could be used to predict the individual's influence on food web dynamics and structure (Brown et al., 2004). Kolar and Lodge (2002) used a trait based approach to predict the likelihood of species to establish, spread and their potential to become a nuisance. Species that were more likely to establish grew relatively faster, but species that were likely to spread grew relatively slower. Future experiments should vary ingestion rates while keeping the diet composition constant to clearly assess the impact of metabolic rate on establishment. Furthermore, it needs to be tested, if similar effects are observed, when model species are introduced with diet compositions that are similar to other nodes. This would be a necessary step towards linking impacts of introductions to species traits.

Additionally, impacts on resilience could be assessed by sequential deletions. Instead of putting a removed node back before the next removal, nodes are removed consecutively. Sequential deletions can be ordered by e.g. body size or trophic position and results can be compared to random sequences. Sequential deletions could also help to identify how much diversity is needed for this food web to remain resilient against further species loss.

7.5 Conclusion

Studies of multi-species assemblages across different trophic levels have been identified as rare and this study attempted to assess impacts of environmental change on a specific ecosystem through a food web model approach. This study follows the

recommendation of the IPCC report (2007) for more hands on approaches to identify areas for conservation. Using food web modelling to identify keystone species and assess impacts of non-native species and climate change on a specific ecosystem is a novel approach to the authors knowledge. The gap between purely theoretical food webs and experimental approaches, was attempted to be bridged by developing a realistic food web model based on empirical data and the consequences of the results in an ecological context was emphasised, rather than solely concentrating on theoretical food web measures.

Modelling studies that attempt to assess impacts of biodiversity and ecosystem function remain rare (Lecerf and Richardson, 2010), but of great importance with the current rates of species loss. A correlation between secondary production and biodiversity could not be identified, but the results suggested resilience to perturbations, such as species introduction. However, whether this resilience is a result of the diversity of the system could not be established and needs to be further investigated.

The existence of keystone species has been controversial and the results of this study suggest that no keystone species exist for the study site. This could be generally true for open, dynamic systems, questioning conservation measures that target single species, rather than using systems approaches that target 'keystone structures'. For example, keystone structures could be defined by certain types of land use (space for riparian vegetation) or un-obstructed pathways for migration to promote a healthy ecosystem that is resilient to perturbations and provides desired ecosystem services.

Appendix A

Food web data

A.1 Length-weight relationships for fishes

Table A.1: Length-weight relationships for fishes and corresponding R^2-values. Column 4 shows length-weight relationships taken from fishbase when $R^2 < 0.9$ for the calculated length-weight relationships.

Species	Length-weight equation calculated	R^2-value	Length-weight equation fishbase
Bullhead (*Cottus gobio*)	$y = 4.0885 \cdot x^{0.5545}$	$R^2 = 0.026$	$y = 0.0066 \cdot x^{3.304}$
Dace (*Leuciscus leuciscus*)	$y = 0.0068 \cdot x^{3.2279}$	$R^2 = 0.9593$	-
Eel (*Anguilla anguilla*)	$y = 0.0314 \cdot x^{2.1746}$	$R^2 = 0.7315$	$y = 0.03 \cdot x^{2.19}$
Gudgeon (*Gobio gobio*)	$y = 0.0067 \cdot x^{3.2307}$	$R^2 = 0.9593$	-
Minnow (*Phoxinus phoxinus*)	-	-	$y = 0.0042 \cdot x^{3.421}$
Pike (*Esox lucius*)	$y = 0.006 \cdot x^{3.0859}$	$R^2 = 0.975$	-
Roach (*Rutilus rutilus*)	$y = 0.0054 \cdot x^{3.3896}$	$R^2 = 0.984$	-
Salmon (*Salmo salar*)	$y = 0.0327 \cdot x^{2.5731}$	$R^2 = 0.9618$	-
Stoneloach (*Barbatula barbatula*)	$y = 0.4539 \cdot x^{1.0643}$	$R^2 = 0.5411$	$y = 0.1264 \cdot x^{1.8775}$
Trout (*Salmo trutta*)	$y = 0.0217 \cdot x^{2.789}$	$R^2 = 0.9227$	-

A.2 Biomass data from macroinvertebrate samples

Table A.2: Macroinvertebrate biomass data from the in 2008 conducted survey. The mean total biomass was 12.32 g m^{-2}.

Sample ID	Date	Patch ID	Time	Weight [g]
S01	30/07/2008	1	6:49	0.644
S02	30/07/2008	2	6:56	0.259
S03	30/07/2008	3	7:08	1.883
S04	30/07/2008	4	7:14	0.070
SO5	30/07/2008	5	7:21	0.949
S06	30/07/2008	6	7:28	1.190
S07	30/07/2008	1	12:26	1.027
S08	30/07/2008	2	12:34	0.531
S09	30/07/2008	3	12:40	0.918
S10	30/07/2008	4	13:32	0.070
S11	30/07/2008	5	13:25	1.269
S12	30/07/2008	6	13:13	1.874
S13	30/07/2008	1	19:09	0.964
S14	30/07/2008	2	19:14	0.542
S15	30/07/2008	3	19:20	1.353
S16	30/07/2008	4	19:24	0.047
S17	30/07/2008	5	19:52	0.751
S18	30/07/2008	6	20:01	1.537
S19	28/08/2008	1	7:05	0.536
S20	28/08/2008	2	7:15	1.777
S21	28/08/2008	3	7:55	1.413
S22	28/08/2008	4	8:00	1.272
S23	28/08/2008	5	8:10	2.106
S24	28/08/2008	6	8:16	1.789
S25	28/08/2008	1	12:25	1.635
S26	28/08/2008	2	12:31	0.664
S27	28/08/2008	3	12:36	1.770
S28	28/08/2008	4	12:59	0.766
S29	28/08/2008	5	13:08	2.917
S30	28/08/2008	6	13:16	1.703
S31	28/08/2008	1	19:20	1.894
S32	28/08/2008	2	19:25	2.238
S33	28/08/2008	3	19:33	2.366
S34	28/08/2008	4	19:56	0.211
S35	28/08/2008	5	20:03	1.452
S36	28/08/2008	6	20:14	1.700

A.3 Food web nodes and starting stock values

Table A.3: Food web nodes, mean weight of the average individual (just fish nodes) and starting stock values.

Node	Abbreviations	Weight [g]	Starting stock value [cal/m^2]
Coleoptera	Col		8
Diptera	Dip		603
Ephemeroptera	Eph		86
Gammaridae	Gam		5813
Mollusca	Mol		1147
Oligochaeta	Oli		1107
Plecoptera	Ple		1
Trichoptera	Tri		211
Bullhead	Bul	1.3	178
Dace	Dac	60.0	6681
Eel_1	Ee1	24.6	1230
Eel_2	Ee2	125.2	1381
Eel_3	Ee3	148.1	2211
Gudgeon	Gud	35,7	329
Minnow	Min	1.7	2272
Pike1	Pi1	97.6	270
Pike2	Pi2	668.1	1108
Pike3	Pi3	2216.9	4086
Roach	Roa	58.3	1128
Salmon	Sal	46.0	3231
Stoneloach	Sto	4.8	870
Trout	Tro	78.6	1924

A.4 Diet compositions

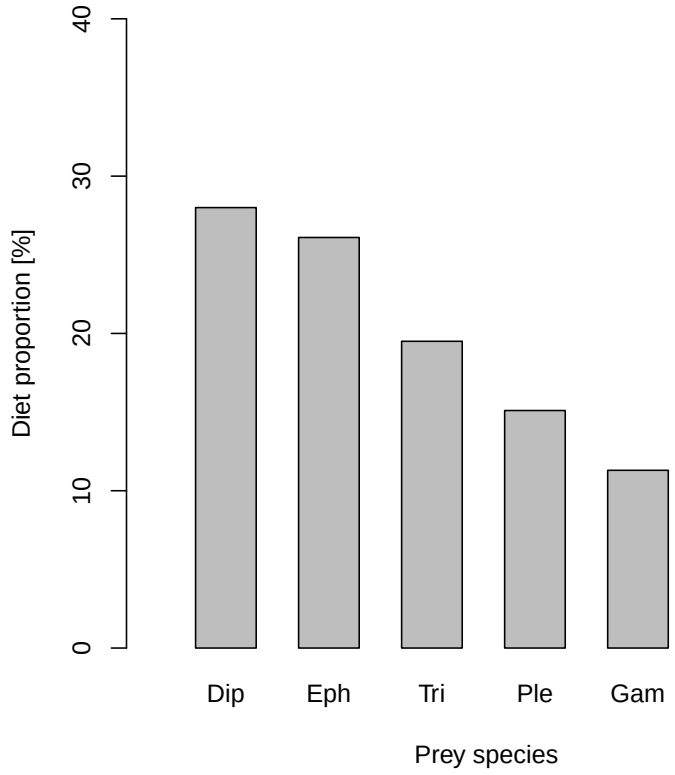

Figure A.1: Diet composition for Bullhead. For abbreviations of prey nodes see Appendix Table A.3.

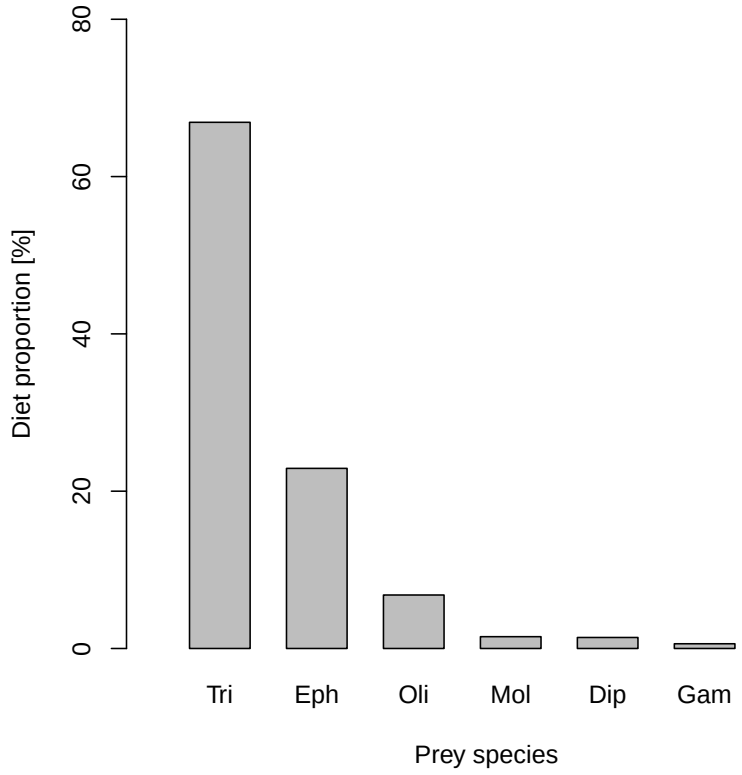

Figure A.2: Diet composition for Dace. For abbreviations of prey nodes see Appendix Table A.3.

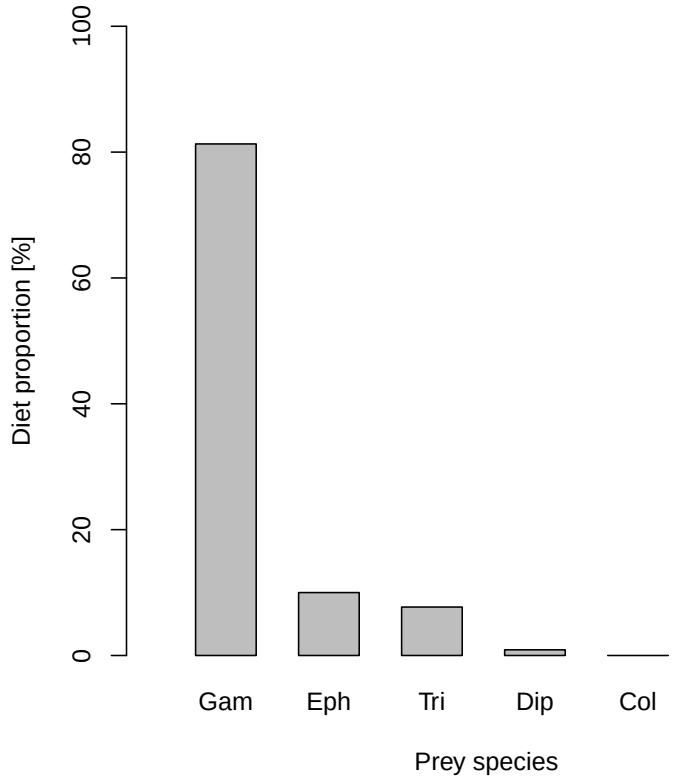

Figure A.3: Diet composition for Eel_1. For abbreviations of prey nodes see Appendix Table A.3.

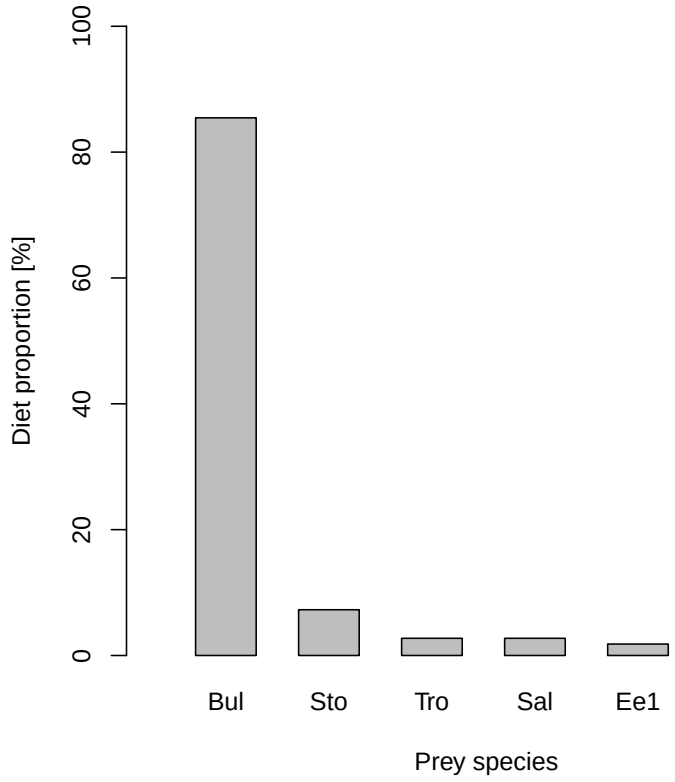

Figure A.4: Diet composition for Eel_2. For abbreviations of prey nodes see Appendix Table A.3.

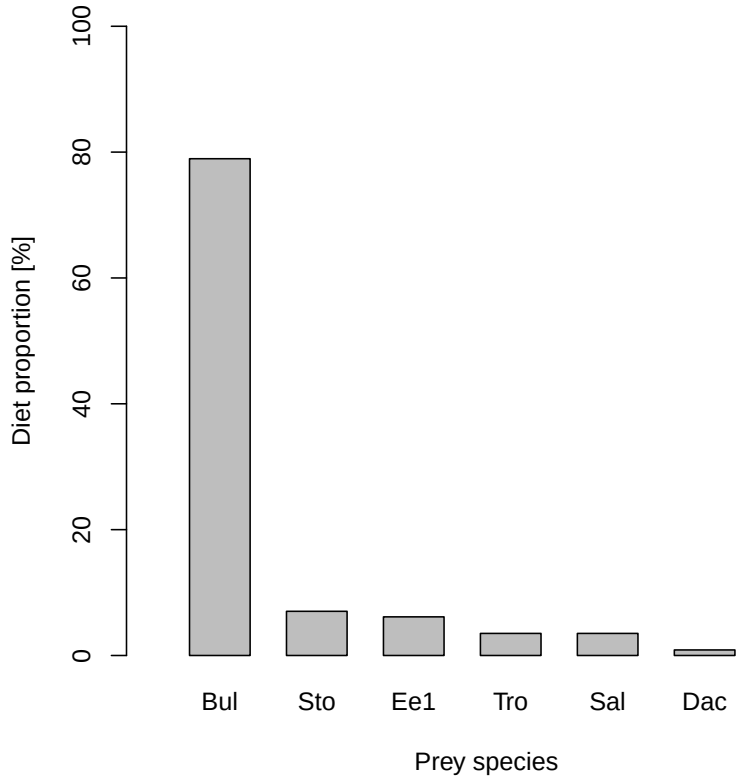

Figure A.5: Diet composition for EEL_3. For abbreviations of prey nodes see Appendix Table A.3.

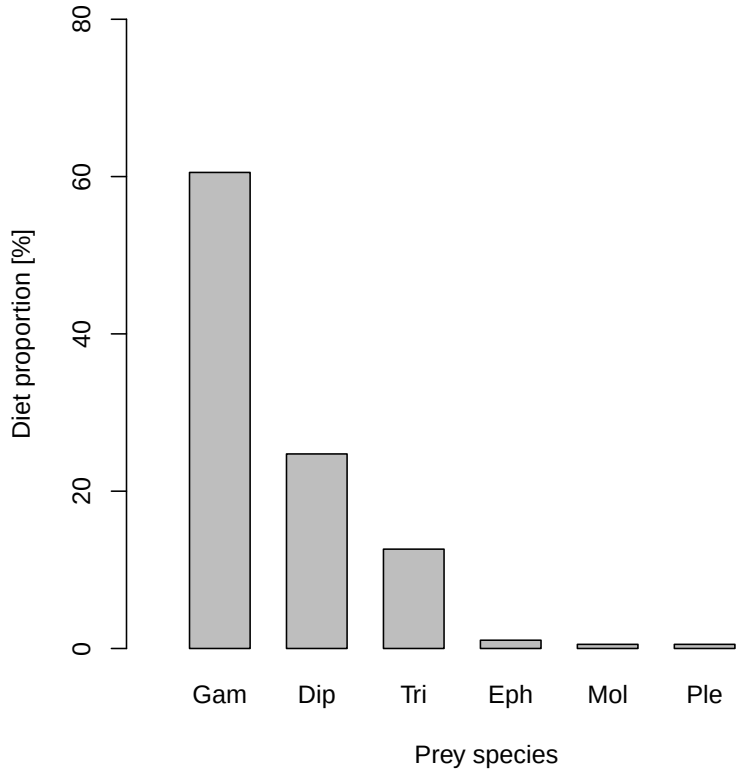

Figure A.6: Diet composition for Gudgeon. For abbreviations of prey nodes see Appendix Table A.3.

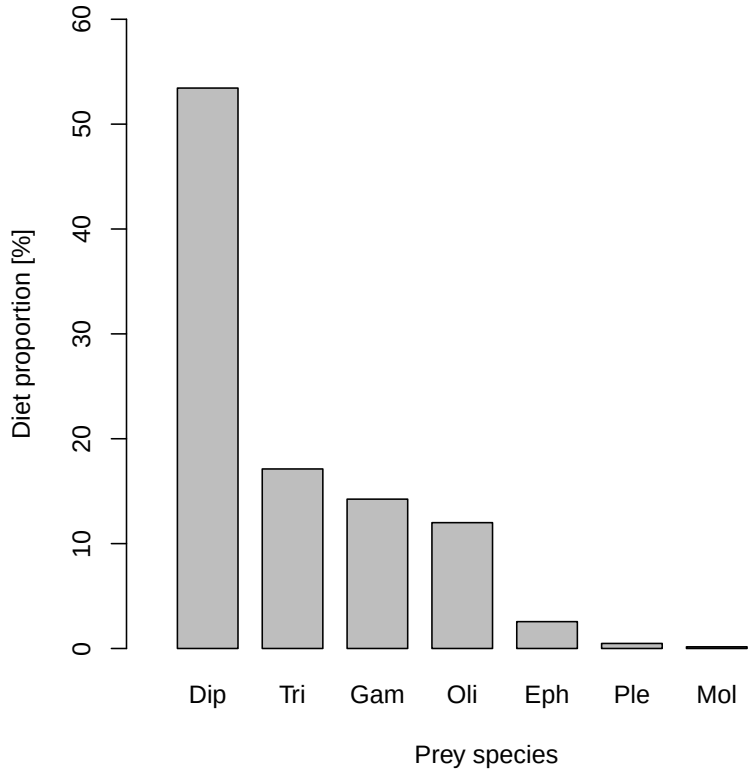

Figure A.7: Diet composition for Minnow. For abbreviations of prey nodes see Appendix Table A.3.

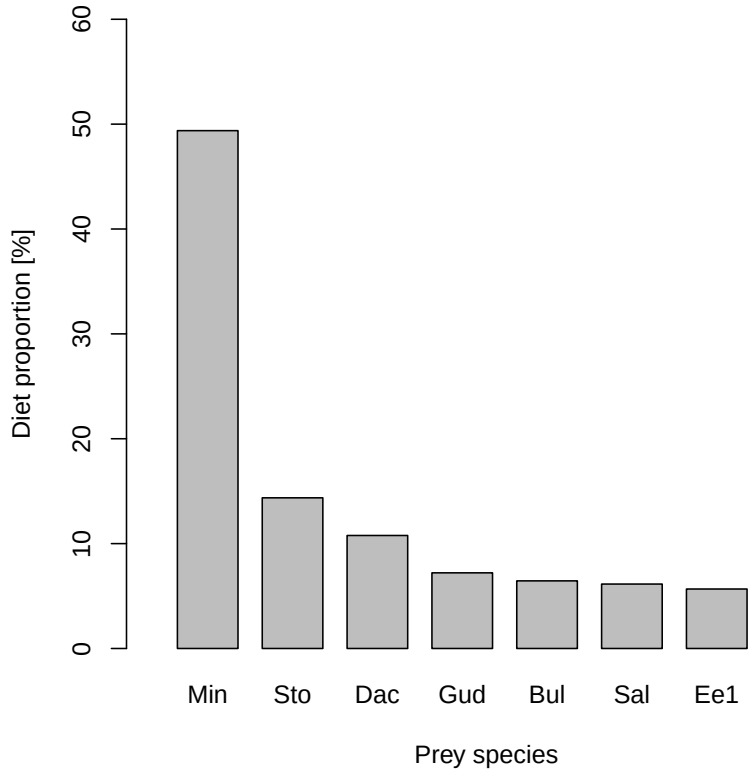

Figure A.8: Diet composition for Pike1. For abbreviations of prey nodes see Appendix Table A.3.

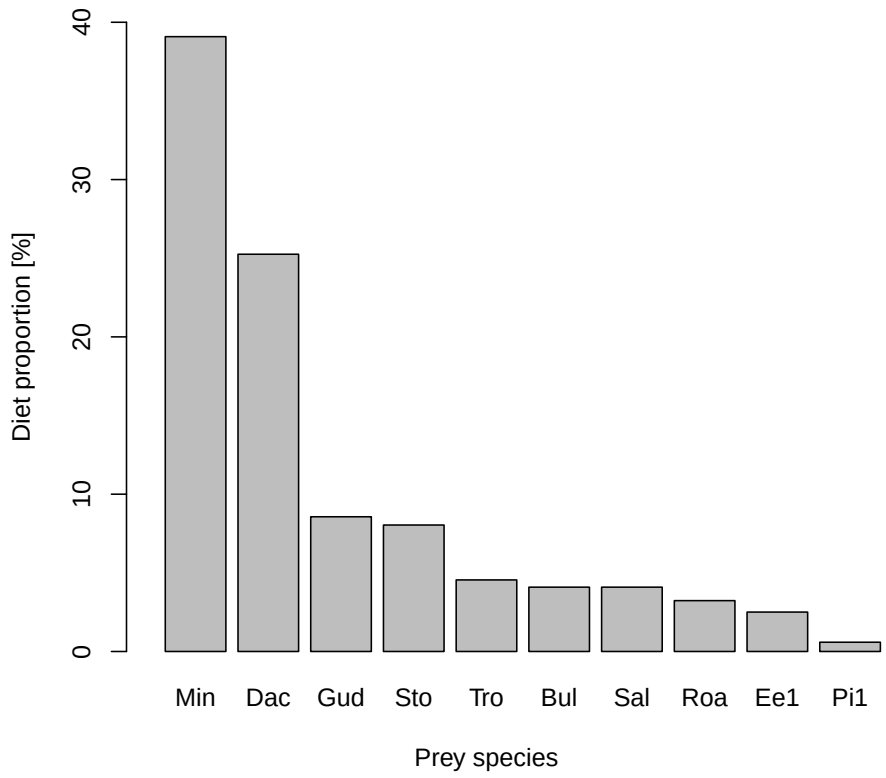

Figure A.9: Diet composition for Pike2. For abbreviations of prey nodes see Appendix Table A.3.

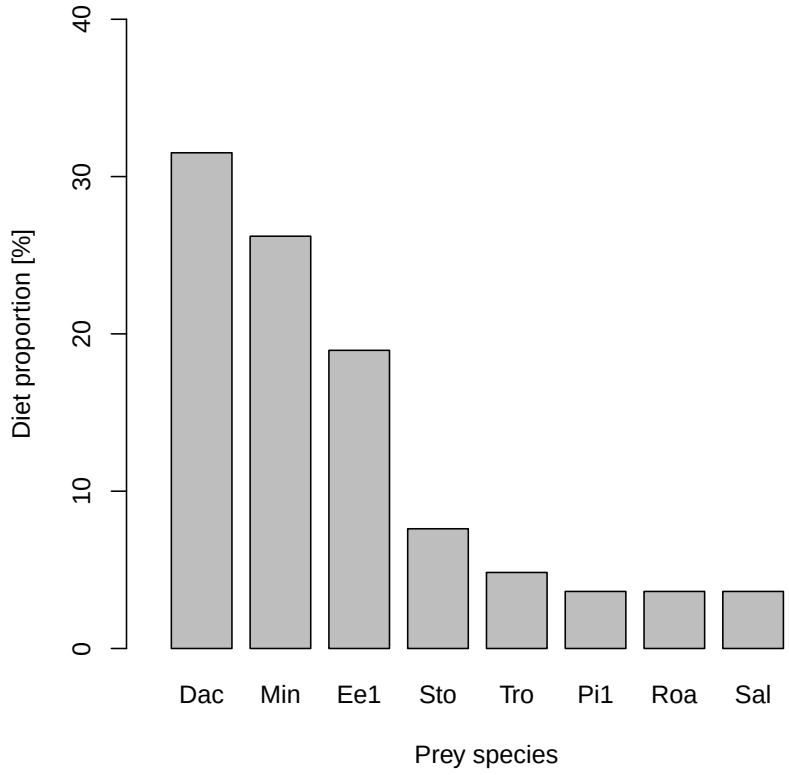

Figure A.10: Diet composition for PIKE3. For abbreviations of prey nodes see Appendix Table A.3.

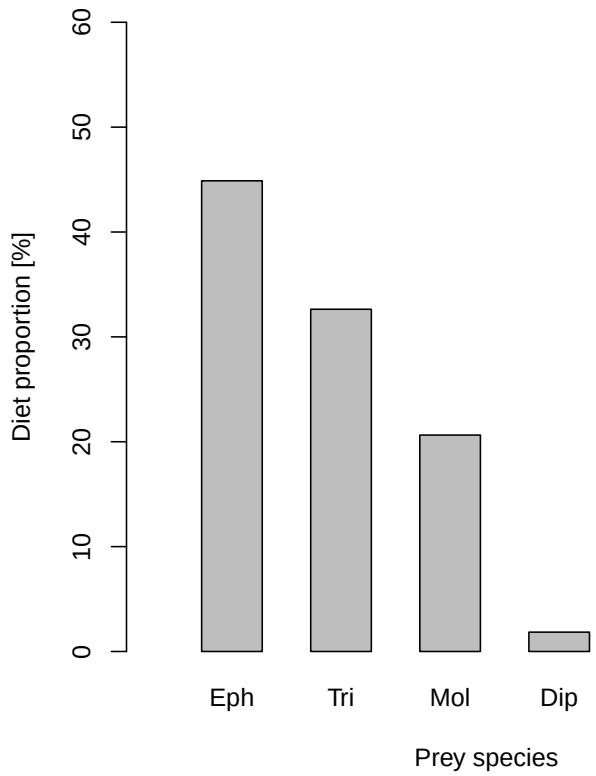

Figure A.11: Diet composition for Roach. For abbreviations of prey nodes see Appendix Table A.3.

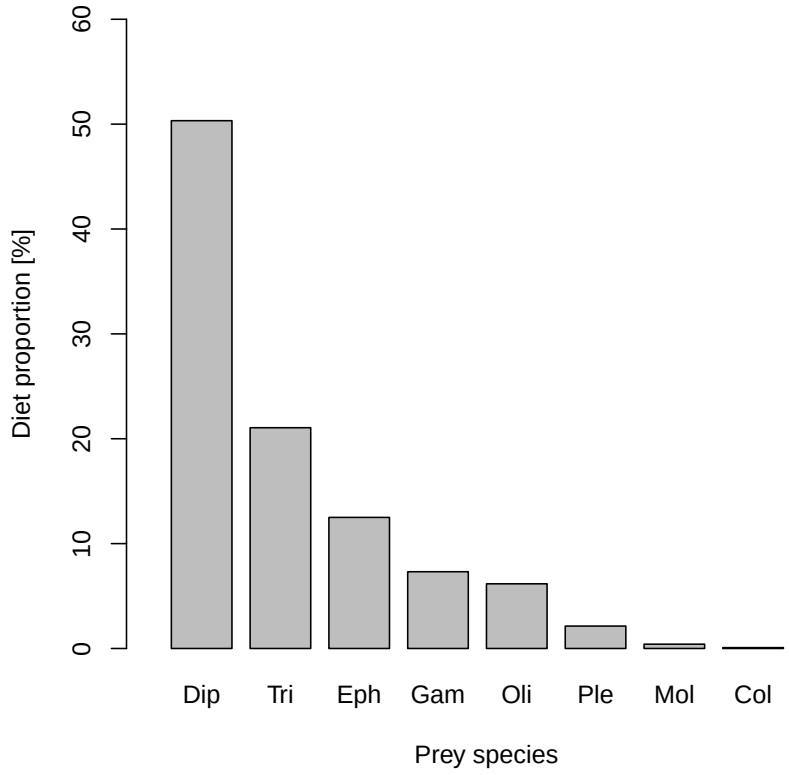

Figure A.12: Diet composition for Salmon. For abbreviations of prey nodes see Appendix Table A.3.

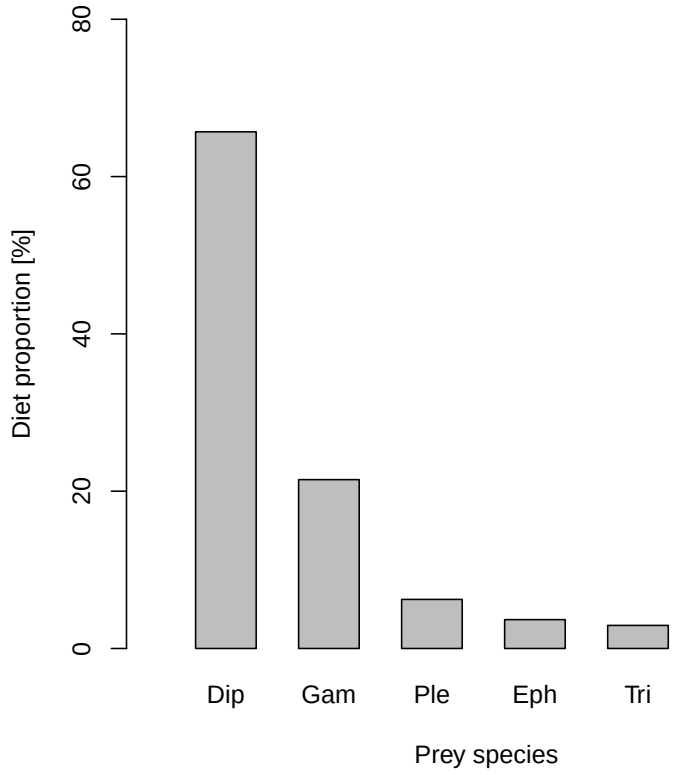

Figure A.13: Diet composition for STONELOACH. For abbreviations of prey nodes see Appendix Table A.3.

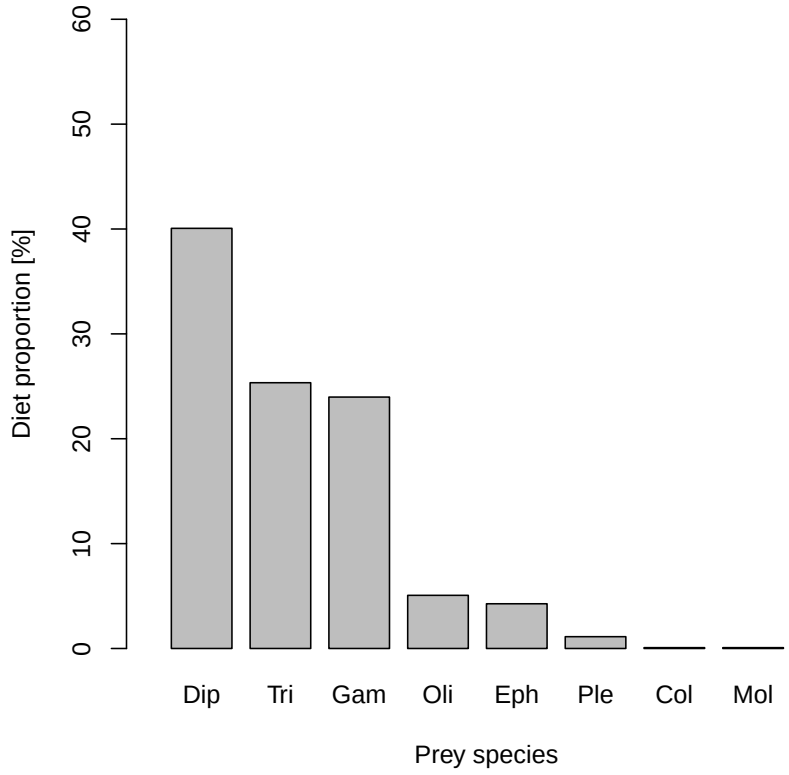

Figure A.14: Diet composition for TROUT. For abbreviations of prey nodes see Appendix Table A.3.

A.5 Additional energy input

Table A.4: Additional energy input that is used for removal experiments. Additional input is the value that was added to the value obtained from calculating energy demand from the metabolic rate. The last column shows the percentage that was added to the the calculated input based on the metabolic rate.

Species node	Additional input	Total input from the environment	Input form the environment based on MR (just invertebrates)	Added percentage of metabolic rate [%]
Coleoptera	6.3	7	0.7	903
Diptera	58	85	27	216
Ephemeroptera	53.4	60	6.6	811
Gammaridae	30	400	370	8
Mollusca	-33	350	383	-9
Oligochaeta	11	70	59	19
Plecoptera	7.9	8	0.1	14138
Trichoptera	88	100	12	724
Bullhead	20	20		312
Salmon	3	3		5
Trout	3	3		9
Minnow	15	15		19
Stoneloach	8	8		33
Dace	5	5		4
Gudgeon	0	0		0
Roach	0	0		0
Pike1	1	1		23
Pike2	1	1		8
Pike3	3	3		8
Eel_1	10	10		39
Eel_2	5	5		23
Eel_3	5	5		15

A.6 Baseline Model - development of the stock values over time

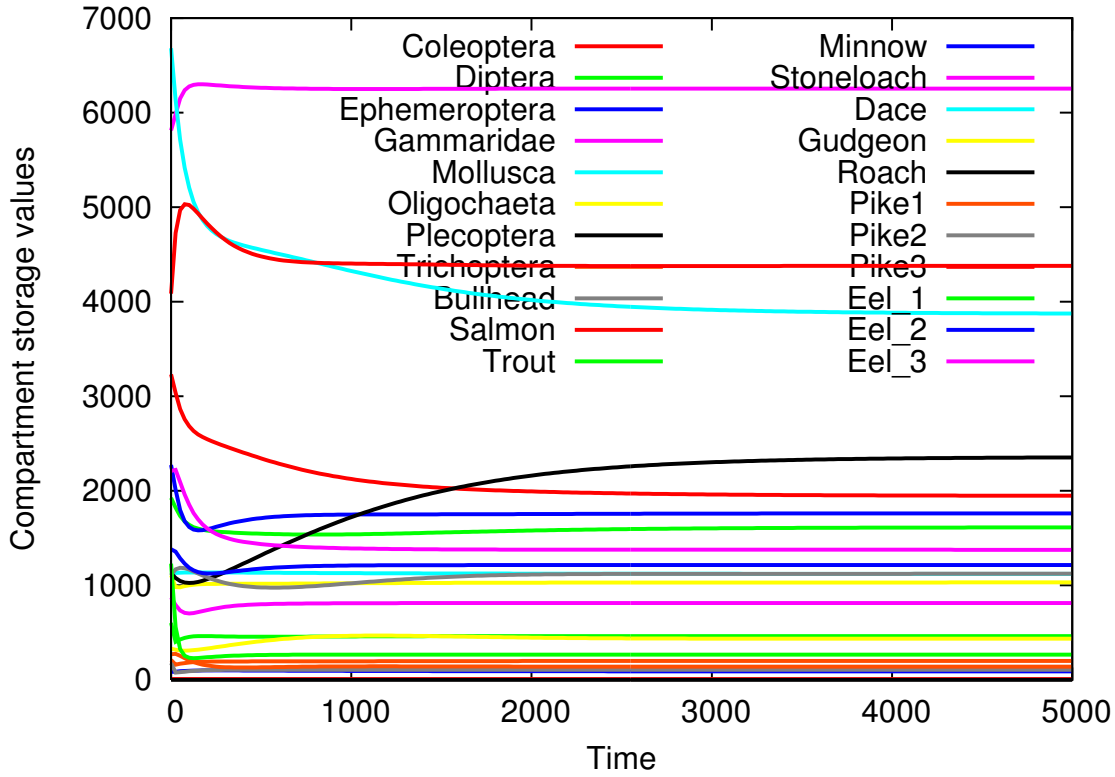

Figure A.15: EcoNet generates a graph that depicts the development of the stock values over time. This one is the output for the Baseline Model.

Appendix B

Methods of gut content analysis

Table B.1: Different methods of stomach content analysis and their strengths and weaknesses (Hyslop, 1980).

Method	Advantage	Disadvantage
Occurrence method The number of stomachs containing one or more individuals from a food category is recorded. This value can be expressed as percentage of all stomachs analysed or all stomachs containing food. Empty stomachs are normally recorded as well.	• simple • quick • requires minimum of apparatus • provides crude qualitative picture of the food spectrum.	• gives little information about relative amounts in one stomach
Numerical method The number of individuals in a food category is recorded. This value can be expressed as percentage of the total individuals in all food categories, or as the mean number of individuals in each food category per stomach.	• simple • fast	• small prey items can be overemphasized • Sometimes numbers cannot be estimated due to the digestion process. • Food items that do not occur in discrete units can not be counted with this method.
Volumetric method Can be either direct or indirect. With direct estimation the displacement of food items or the settled volume is measured with some graduated settling device. With indirect estimation food items are compared with blocks of known volume. This method is used when small items prevail.The value of the volume of a food category is usually given as a percentage of the total volume of all stomach contents. Sometimes only stomachs of a particular fullness are taken into account. The volumetric method is useful to indicate seasonal changes in feeding activity.	• most representative measure of bulk • Can be applied to all food items	• Water might be trapped within the item when using the displacement method, leading to large errors.

Appendix C

Model parameters and methods

C.1 Methods for the calculation of the differential equations

The user has got the choice of method between *i*) Adaptive Time Step (Runge-Kutta-Fehlberg), *ii*) Fixed Time Step (4th order Runge-Kutta) and *iii*) Stochastic (Langevin) method to solve the differential equations. The Adaptive Time Step and the Fixed Time Step methods are both deterministic methods, i.e producing the same output with identical starting conditions.

Adaptive Time Step: The Adaptive Time Step method continuously adjusts the accuracy for the numerical solution of the differential equations based on the complexity of the differential equations. The amount of error allowed between the actual solution and the numerical solution is defined by the *Sensitivity* parameter, which can be adjusted by the the user. Smaller values for *Sensitivity* are more accurate, but require longer computation time. In many cases a higher Sensitivity parameter does not change the final steady state. The parameter *Maximum Time* defines the simulation length.

Fixed Time Step: In comparison to the adaptive time step method, the fixed step method does not adjust its accuracy, but is fixed by the parameter *Step-size* throughout the simulation. *Step-size* complies with the *Sensitivity* parameter, because both are a limit of the allowed error. The adaptive time step method is favoured over the fixed time step method, because it is generally faster and more accurate. However, there might be cases when the user needs more control over the numerical solution. Instead of *Maximum Time* the parameter for simulation length is called *Total Time*.

Stochastic: Stochastic methods incorporate probabilistic behaviour and generates different solutions on each occasion. The adjustable parameters are the same as for the fixed time step method. Only systems that are probabilistic in nature (e.g. ecosystems) should be modelled with this method. The strength of this method is that it shows different outcomes to identical starting conditions, providing an indication whether there is more than one stable state for the system. The stochastic method used by EcoNet is based on the Langevin equation (Gillespie, 2000). It is a true stochastic method and should not be confused with a deterministic solution with added noise (Gardiner, 1985; Gillespie, 1992; 2000).

For the removal experiments the adaptive time step method was chosen. Simulations were run with the Baseline Model to assess the influence of model parameters such as time steps and sensitivity.

C.2 Model parametrisation

***Max Time Steps* parameter** The calculations in the model are based on time steps. Therefore flow rates have to be normalised to the same timescale (e.g. daily consumption). The output of the model that depicts the values of the compartments over time should not be confused with a projection of the development of stock values over a certain period (e.g. year), but rather indicates if the system reaches a stable

state, which is necessary to proceed with species removal. In the real food web species abundance changes seasonally, but in the model mean values over the year are used. Therefore, seasonal patterns are not reflected. The model will predict how the removal of species propagates through the system and how that influences the abundance of other species. It does not attempt to give an account of the exact development of species abundance on a day to day scale.

The choice of time steps mainly depends on when the stable state is reached. Stopping the simulation at an earlier point might result in different values. The parameter *Max Time Steps* was adjusted accordingly in all modelling trials.

***Sensitivity* parameter** The Adaptive Time Step method continuously adjusts its accuracy based on the complexity of the differential equations. The amount of error allowed is defined by the *Sensitivity* parameter, which can be adjusted by the the user, before the model is run. Smaller values for *Sensitivity* are more accurate, but require longer computation time. The Baseline Model without additional energy input was run with sensitivity values of 0.01, 0.05, 0.1, and 10.0, but no influence on the final stock values was found.

C.3 Energy assimilation efficiency

The energy available to the organism is dependent on the digestion efficiency of a particular food source, the rest is excreted as faeces. An organism invests that energy into: maintenance, digestion, activity, growth , allocation of reserves, and reproduction. Only the energy invested into biomass is available to the next higher trophic level. In general only 5 to 20% of the energy of one trophic level is available to the next trophic level (Cragg, 1969; White, 1992). In the model this is reflected by an outflow rate from each organism into the environment. The range of the outflow rate (80 to 95% of the stock value) provides room for adjustments to stabilise the model. The removals are run with 90% assimilation efficiency for all species. The outflow rate is calculated in the following way:

$c_{outflow} = 0.9 \cdot \frac{I}{A}$, with A: starting stock value predator [cal], I: ingestion rate [cal d m^{-2}].

Variation of energy assimilation efficiency Dependent on the food source this assimilation energy may vary. To assess the influence of higher assimilation rates the Baseline Model (without additional energy input) was run with outflow rates based on 20 and 30 % assimilation rates. In the model runs with higher assimilation efficiency most of the energy gets assigned to PIKE2, but also TROUT benefits. The model was also run with mixed outflow rates. Variation of the energy assimilation efficiency did not result in less extinctions and was not sufficient to achieve a model output that resembles the original food web closely enough.

Appendix D

Additional results for removals

D.1 Removals from the natural communities

Autumn 2003

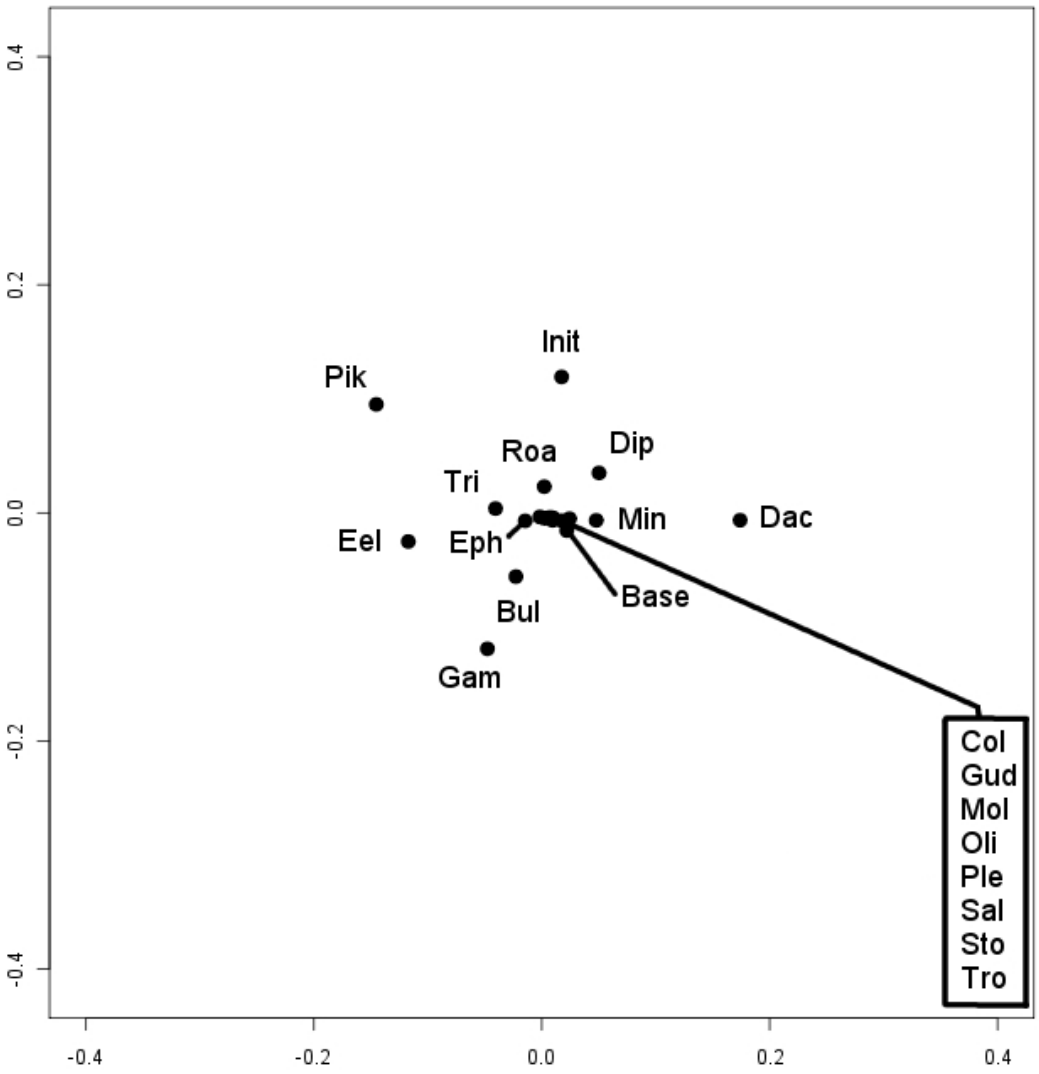

Figure D.1: MDS-ordination for removals from baseline community Autumn '03. For abbreviations of prey nodes see Appendix Table A.3. Stress: 10.25%.

Autumn 2004

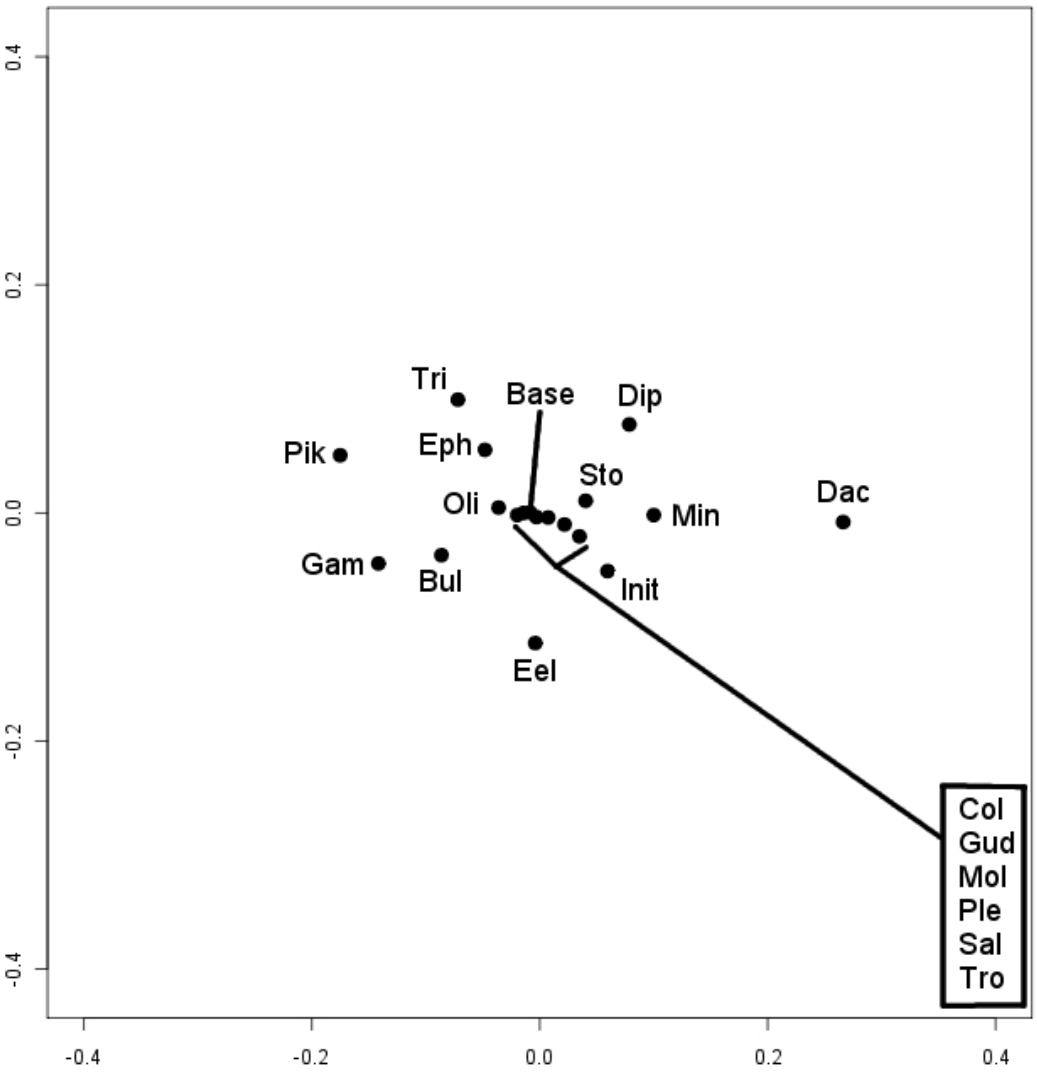

Figure D.2: MDS-ordination for removals from baseline community Autumn '04. For abbreviations of prey nodes see Appendix Table A.3. Stress: 9.44%.

Autumn 2005

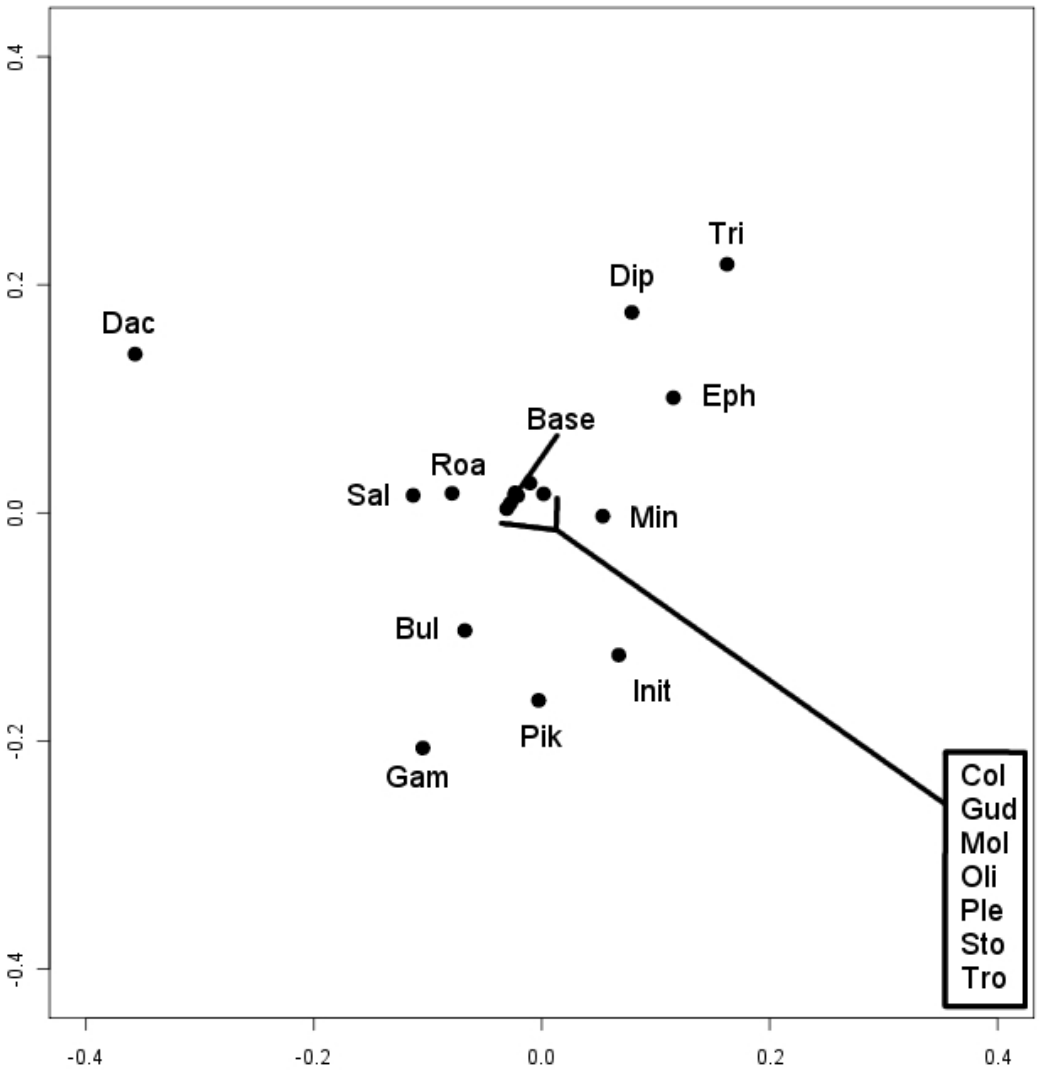

Figure D.3: MDS-ordination for removals from baseline community Autumn '05. For abbreviations of prey nodes see Appendix Table A.3. Stress: 10.92%.

D.2 Relative change of abundance in the remaining nodes after species removal

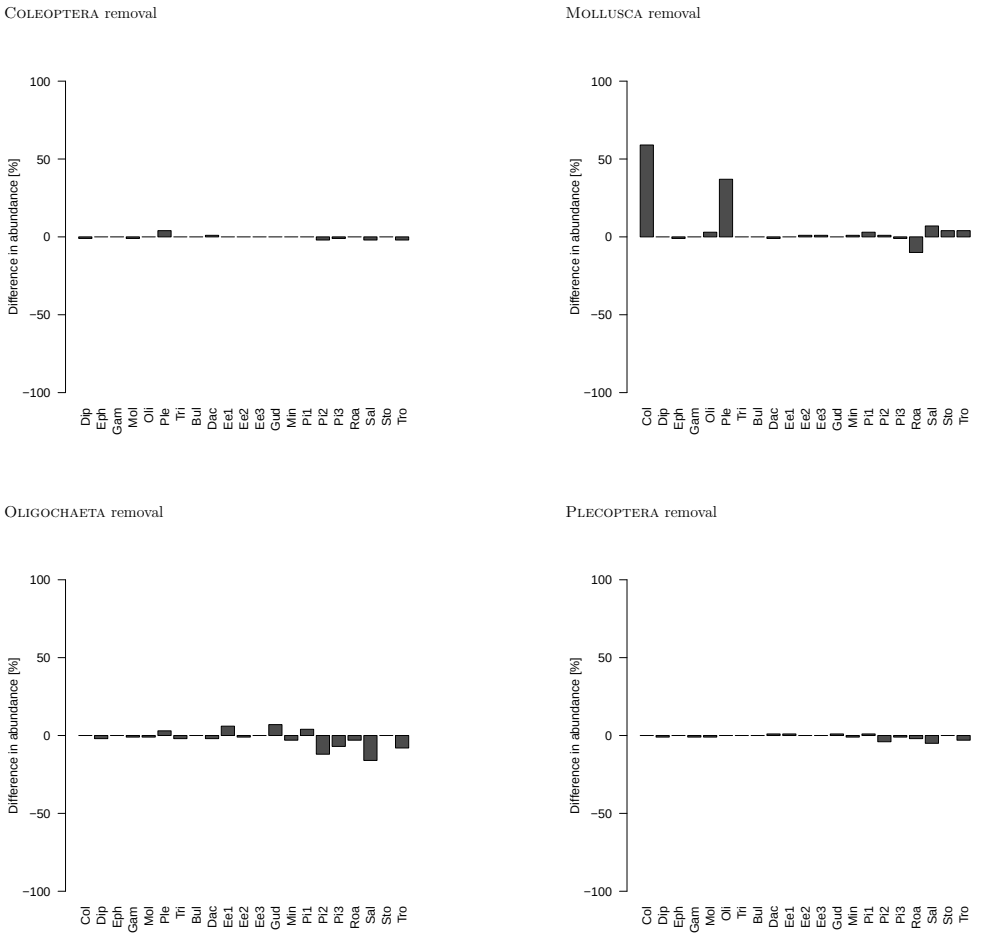

Figure D.4: Impact of the removal of the macroinvertebrate nodes Coleoptera, Mollusca, Oligochaeta and Plecoptera on the abundance of the remaining nodes, relative to the Baseline model. For abbreviations of prey nodes see Appendix Table A.3.

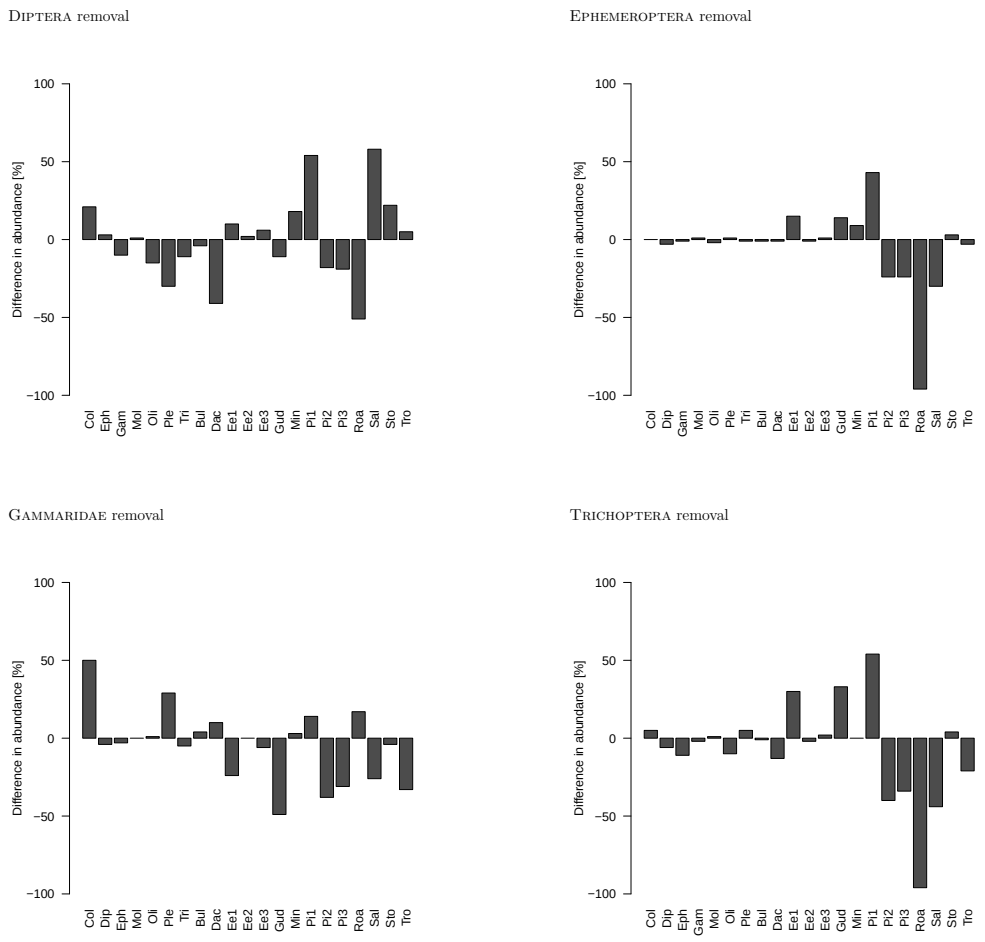

Figure D.5: Impact of the removal of the macroinvertebrate nodes Diptera, Ephemeroptera, Gammaridae and Trichoptera on the abundance of the remaining nodes, relative to the Baseline model. For abbreviations of prey nodes see Appendix Table A.3.

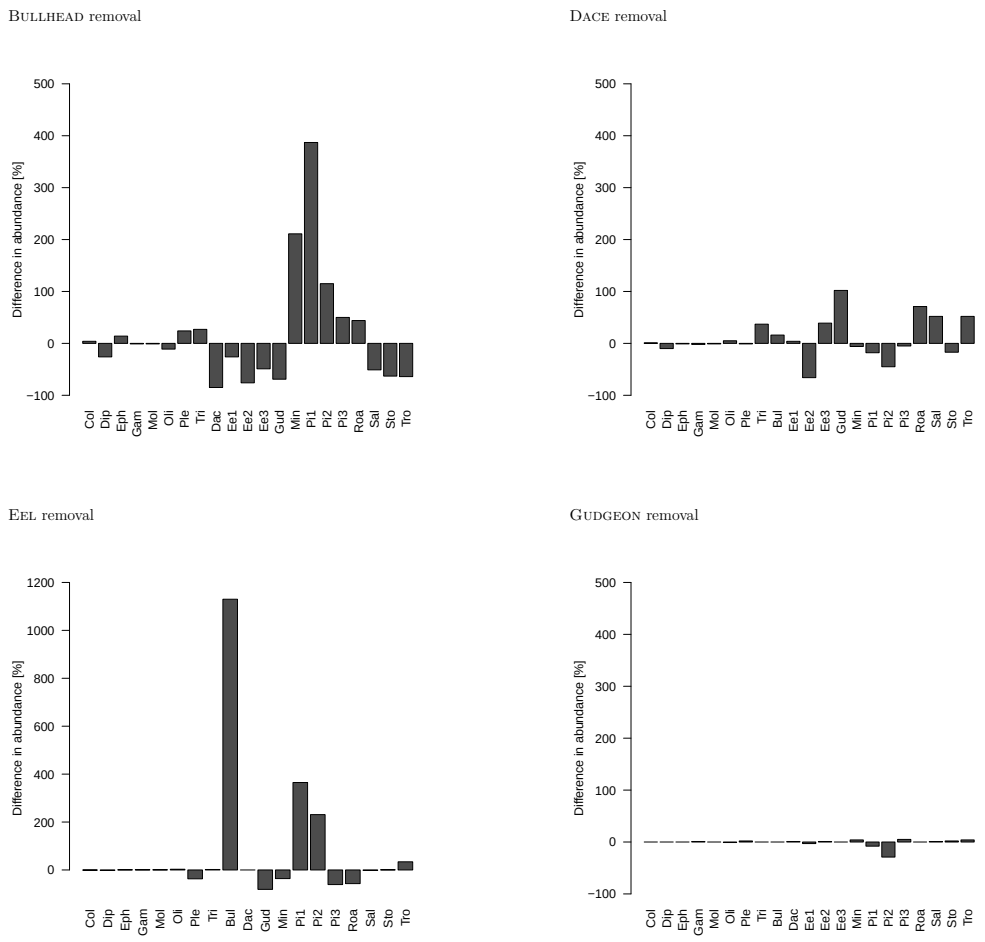

Figure D.6: Impact of the removal of the fish nodes Bullhead, Dace, Eel, and Gudgeon on the abundance of the remaining nodes, relative to the Baseline model. For abbreviations of prey nodes see Appendix Table A.3.

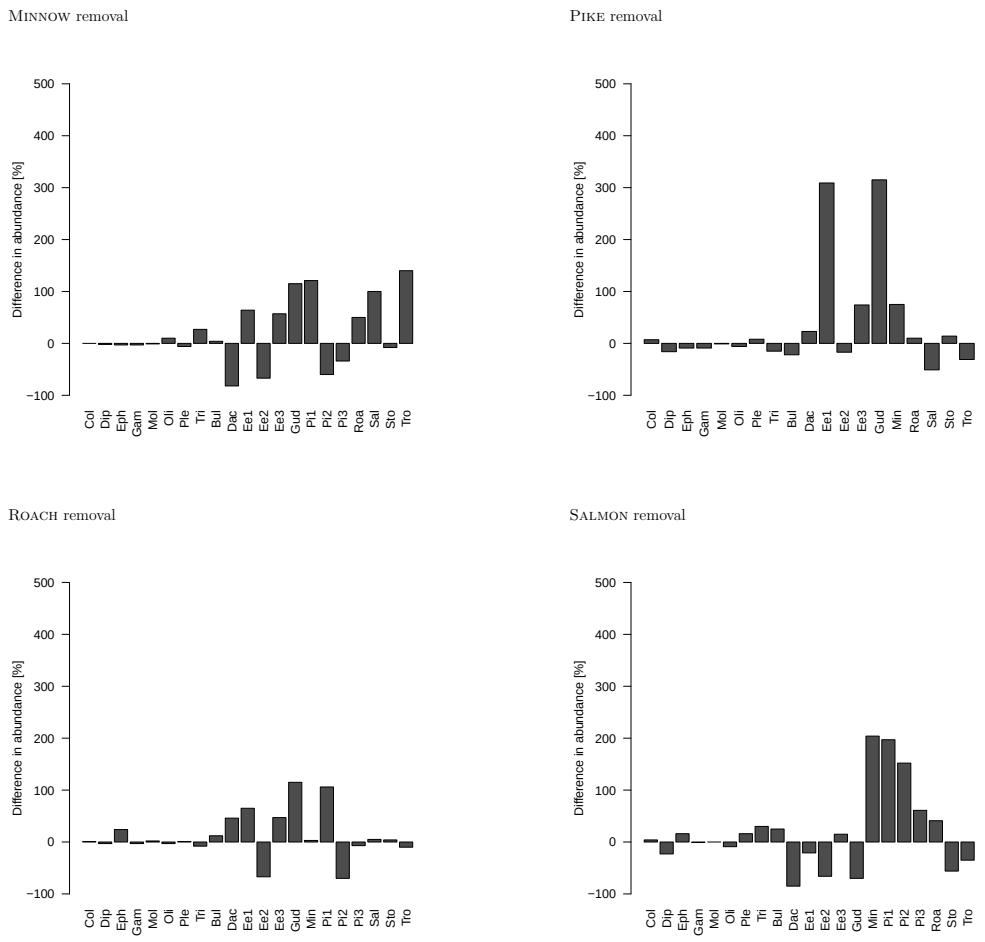

Figure D.7: Impact of the removal of the fish nodes Minnow, Pike, Roach and Salmon on the abundance of the remaining nodes, relative to the Baseline model. For abbreviations of prey nodes see Appendix Table A.3.

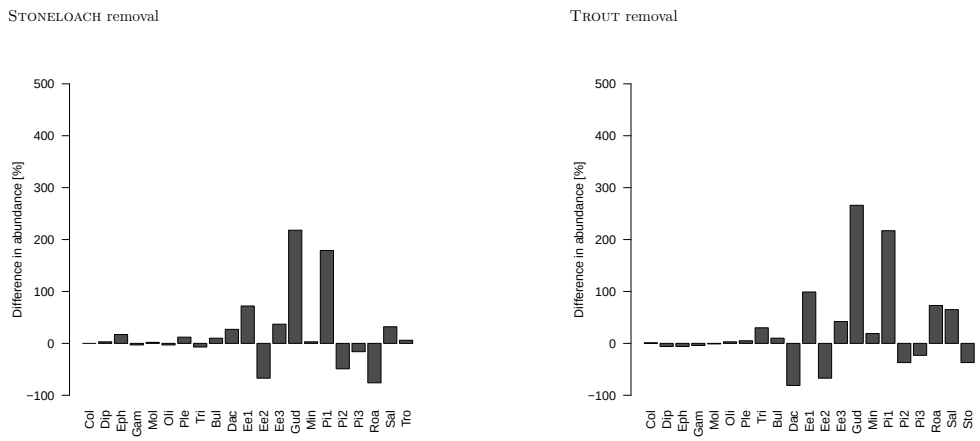

Figure D.8: Impact of the removal of the fish nodes Stoneloach and Trout on the abundance of the remaining nodes, relative to the Baseline model. For abbreviations of prey nodes see Appendix Table A.3.

Bibliography

Abarca-Arenas, L. G. and Ulanowicz, R. E. (2002). The effects of taxonomic aggregation on network analysis. *Ecological Modelling*, 149(3):285–296.

Adamicka, P. S. (1991). A Food Schedule for Cottus-Gobio L (Pisces) in Oberer-Seebach, Ritrodat-Lunz Study Area, Austria. *International Association of Theoretical and Applied Limnology*, 24:1941–1943.

Adams, J. (1993). A review of the NRA Anglian Region Zander Cull Policy. Unpublished document available from Environment Agency, Kingfisher House, Goldhay Way, Orton Goldhay, Peterborough PE2 0ZR, United Kingdom.

Akbari, M., Murphy, S., Kay, J., and Swanton, C. (1999). Energy-Bases Indicators of (Agro)Ecosystem Health. In Quattrochi, D. and Luvall, J., editors, *Thermal Remote sensing in Land Surface Processes*. Ann Arbor Press.

Allan, J. D. (2004). Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology Evolution and Systematics*, 35:257–284.

Allan, J. D., Palmer, M., and Poff, N. L. (2005). Climate change and freshwater ecosystems. In *Climate change and biodiversity*, pages 274–295. Yale University Press, New Haven & London.

Allesina, S., Bondavalli, C., and Scharler, U. M. (2005). The consequences of the aggregation of detritus pools in ecological networks. *Ecological Modelling*, 189:221–232.

Amoros, C., Rostan, J. C., Pautou, G., and Bravard, J. P. (1987). The reversible

process concept applied to the environmental-management of large river systems. *Environmental Management*, 11(5):607–617.

Anderson, M. J. and Willis, T. J. (2003). Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. *Ecology*, 84(2):511–525.

Arlinghaus, R., Mehner, T., and Cowx, I. G. (2002). Reconciling traditional inland fisheries management and sustainability in industrialized countries, with emphasis on Europe. *Fish and Fisheries*, 3(4):261–316.

Atkinson, D. (1994). Temperature and Organism Size - A Biological Law For Ectotherms. *Advances In Ecological Research, Vol 25*, 25:1–58.

Baensch, H. and Riehl, R. (1991). *Aquarien atlas*, volume Bd. 3. Mergus, Verlag für Natur- und Heimtierkunde, Melle, Germany.

Baird, D., Fath, B. D., Ulanowicz, R. E., Asmus, H., and Asmus, R. (2009). On the consequences of aggregation and balancing of networks on system properties derived from ecological network analysis. *Ecological Modelling*, 220(23):3465–3471.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D., and Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9(10):1146–1156.

Baras, E. (1994). Constraints Imposed By High-densities On Behavioral Spawning Strategies In the Barbel, Barbus-barbus. *Folia Zoologica*, 43(3):255–266.

Baron, J. S., Poff, N. L., Angermeier, P. L., Dahm, C. N., Gleick, P. H., Hairston, N. G., Jackson, R. B., Johnston, C. A., Richter, B. D., and Steinman, A. D. (2002). Meeting ecological and societal needs for freshwater. *Ecological Applications*, 12(5):1247–1260.

Baxter, C. V., Fausch, K. D., Murakami, M., and Chapman, P. L. (2004). Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, 85(10):2656–2663.

Baxter, C. V., Fausch, K. D., and Saunders, W. C. (2005). Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, 50(2):201–220.

Bejan, A. (1997). *Advanced Engineering Thermodynamics*. John Wiley and sons, New York.

Belgrano, A., Scharler, U. M., Dunne, J., and Ulanowicz, R. E. (2005). *Aquatic Food Webs An Ecosystem Approach*. Oxford University Press.

Bender, E. A., Case, T. J., and Gilpin, M. E. (1984). Perturbation Experiments In Community Ecology - Theory and Practice. *Ecology*, 65(1):1–13.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., and Nystrom, M. (2003). Reserves, resilience and dynamic landscapes. *Ambio*, 32(6):389–396.

Benke, A. C. (1993). Concepts and Patterns of Invertebrate Production In Running Waters. *International Association of Theoretical and Applied Limnology - Proceedings, Vol 25, Pt 1*, 25:15–38.

Benke, A. C. (1998). Production dynamics of riverine chironomids: Extremely high biomass turnover rates of primary consumers. *Ecology*, 79(3):899–910.

Benke, A. C., Hauer, F. R., Stites, D. L., Meyer, J. L., and Edwards, R. T. (1992). Growth of Snag-dwelling Mayflies In A Blackwater River - the Influence of Temperature and Food. *Archiv Fur Hydrobiologie*, 125(1):63–81.

Benke, A. C., Huryn, A. D., Smock, L. A., and Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *J. N. Am. Benthol. Soc.*, 18(3):308–343.

Benke, A. C. and Wallace, J. B. (1997). Trophic basis of production among riverine caddisflies: Implications for food web analysis. *Ecology*, 78(4):1132–1145.

Benstead, J. P., March, J. G., Pringle, C. M., Ewel, K. C., and Short, J. W. (2009). Biodiversity and ecosystem function in species-poor communities: community structure and leaf litter breakdown in a Pacific island stream. *Journal of the North American Benthological Society*, 28(2):454–465.

Berg, L. (1964). *Freshwater fishes of the U.S.S.R. and adjacent countries*, volume 2. Israel Program for Scientific Translations Ltd, Jerusalem, 4 edition.

Berlow, E. L. (1999). Strong effects of weak interactions in ecological communities. *Nature*, 398(6725):330.

Berlow, E. L., Brose, U., and Martinez, N. D. (2008). The "Goldilocks factor" in food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 105(11):4079–4080.

Berlow, E. L., Navarrete, S. A., Briggs, C. J., Power, M. E., and Menge, B. A. (1999). Quantifying variation in the strengths of species interactions. *Ecology*, 80(7):2206–2224.

Berlow, E. L., Neutel, A. M., Cohen, J. E., de Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen, V. A. A., Jones, J. I., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M., and Petchey, O. (2004). Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, 73(3):585–598.

Berrie, A. (1976). Detritus microorganisms and animals in fresh water. In Anderson, J. M. and Macfadyen, A., editors, *The Role Of Terrestrial And Aquatic Organisms In Decomposition Processes*, volume 17, page 1977, Oxford, England. British Ecological Society Symposium, Blackwell Scientific Publications.

Berrie, A. D. (1992). The Chalk-Stream Environment. *Hydrobiologia*, 248(1):3–9.

Berryman, A. A. (1991). Stabilization Or Regulation - What It All Means. *Oecologia*, 86(1):140–143.

Bianco, P. G. (1998). Diversity of Barbinae fishes in southern Europe with descrip-

tion of a new genus and a new species (Cyprinidae). *Italian Journal of Zoology*, 65(1 supp 1):125–136.

Bianco, P. G. and Ketmaier, V. (2001). Anthropogenic changes in the freshwater fish fauna of Italy, with reference to the central region and Barbus graellsii, a newly established alien species of Iberian origin. *Journal of Fish Biology*, 59:190–208.

Blanc, G. (1997). Introduced pathogens in European aquatic ecosystems: Theoretical aspects and realities. *Bulletin Francais de la Peche et de la Pisciculture*, (344-45):489–513.

Blanchet, S., Grenouillet, G., Beauchard, O., Tedesco, P. A., Leprieur, F., Durr, H. H., Busson, F., Oberdorff, T., and Brosse, S. (2010). Non-native species disrupt the worldwide patterns of freshwater fish body size: implications for Bergmann's rule. *Ecology Letters*, 13(4):421–431.

Blindow, I., Andersson, G., Hargeby, A., and Johansson, S. (1993). Long-term Pattern of Alternative Stable States In 2 Shallow Eutrophic Lakes. *Freshwater Biology*, 30(1):159–167.

Blondel, J. (2003). Guilds or functional groups: does it matter? *Oikos*, 100(2):223–231.

Bond, N. R., Lake, P. S., and Arthington, A. H. (2008). The impacts of drought on freshwater ecosystems: an Australian perspective. *Hydrobiologia*, 600:3–16.

Bond, W. J. (1993). In *Biodiversity and ecosystem function*, pages 237–253. Springer-Verlag, Berlin, Germany.

Borer, E. T., Anderson, K., Blanchette, C. A., Broitman, B., Cooper, S. D., Halpern, B. S., Seabloom, E. W., and Shurin, J. B. (2002). Topological approaches to food web analyses: a few modifications may improve our insights. *Oikos*, 99(2):397–401.

Borer, E. T., Seabloom, E. W., Shurin, J. B., Anderson, K. E., Blanchette, C. A., Broitman, B., Cooper, S. D., and Halpern, B. S. (2005). What determines the strength of a trophic cascade? *Ecology*, 86(2):528–537.

Borrvall, C., Ebenman, B., and Jonsson, T. (2000). Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters*, 3(2):131–136.

Bracken, M. E. S. and Stachowicz, J. J. (2006). Seaweed diversity enhances nitrogen uptake via complementary use of nitrate and ammonium. *Ecology*, 87(9):2397–2403.

Brander, K. M. (1995). The Effect Of Temperature On Growth Of Atlantic Cod (Gadus-Morhua L). *Ices Journal Of Marine Science*, 52(1):1–10.

Britton, J. R., Brazier, M., Davies, G. D., and Chare, S. I. (2008). Case studies on eradicating the Asiatic cyprinid Pseudorasbora parva from fishing lakes in England to prevent their riverine dispersal. *Aquatic Conservation-marine and Freshwater Ecosystems*, 18(6):867–876.

Britton, J. R., Cucherousset, J., Davies, G. D., Godard, M. J., and Copp, G. H. (2010a). Non-native fishes and climate change: predicting species responses to warming temperatures in a temperate region. *Freshwater Biology*, 55(5):1130–1141.

Britton, J. R., Cucherousset, J., Grey, J., and Gozlan, R. E. (2011). Determining the strength of exploitative competition from an introduced fish: roles of density, biomass and body size. *Ecology of Freshwater Fish*, 20(1):74–79.

Britton, J. R., Davies, G. D., and Brazier, M. (2010b). Towards the successful control of the invasive Pseudorasbora parva in the UK. *Biological Invasions*, 12(1):125–131.

Britton, J. R., Davies, G. D., Brazier, M., and Pinder, A. C. (2007). A case study on the population ecology of a topmouth gudgeon (Pseudorasbora parva) population in the UK and the implications for native fish communities. *Aquatic Conservation-marine and Freshwater Ecosystems*, 17(7):749–759.

Britton, J. R., Davies, G. D., and Harrod, C. (2010c). Trophic interactions and consequent impacts of the invasive fish Pseudorasbora parva in a native aquatic foodweb: a field investigation in the UK. *Biological Invasions*, 12(6):1533–1542.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7):1771–1789.

Brzustowski, T. A. and Golem, P. J. (1977). 2nd-law Analysis of Energy Processes .1. Exergy - Introduction. *Transactions of the Canadian Society For Mechanical Engineering*, 4(4):209–218.

Bystrom, P., Karlsson, J., Nilsson, P., Van Kooten, T., Ask, J., and Olofsson, F. (2007). Substitution of top predators: effects of pike invasion in a subarctic lake. *Freshwater Biology*, 52(7):1271–1280.

Cairns, J. (1977). Quantification of biological integrity. In Ballentine, R. K.; Guarraia, L. J., editor, *The integrity of water*, pages 171–187. U.S. Environmental Protection Agency, Office of Water and Hazardous Materials, Washington, D.C., USA.

Cardinale, B. J., Nelson, K., and Palmer, M. A. (2000). Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos*, 91(1):175–183.

Cardinale, B. J., Palmer, M. A., Ives, A. R., and Brooks, S. S. (2005). Diversity-productivity relationships in streams vary as a function of the natural disturbance regime. *Ecology*, 86(3):716–726.

Cardinale, B. J., Wright, J. P., Cadotte, M. W., Carroll, I. T., Hector, A., Srivastava, D. S., Loreau, M., and Weis, J. J. (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences of the United States of America*, 104(46):18123–18128.

Carpenter, S. R. (1996a). Drivers and dynamics of changes in biodiversity. In (UNEP), U. N. E. P., editor, *Global biodiversity assessment*, pages 311–318. Cambridge University Press, Cambridge, United Kingdom.

Carpenter, S. R. (1996b). Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology*, 77(3):677–680.

Carpenter, S. R. and Cottingham, K. L. (1997). Resilience and restoration of lakes. *Conservation Ecology (online)*, 1(1).

Carpenter, S. R. and Kitchell, J. F. (1996). *The Trophic Cascade in Lakes*. Cambridge University Press.

Carpenter, S. R. and Lodge, D. M. (1986). Effects of Submersed Macrophytes On Ecosystem Processes. *Aquatic Botany*, 26(3-4):341–370.

Carpenter, S. R., Ludwig, D., and Brock, W. A. (1999). Management of eutrophication for lakes subject to potentially irreversible change. *Ecological Applications*, 9(3):751–771.

Cederholm, C. J., Kunze, M. D., Murota, T., and Sibatani, A. (1999). Pacific salmon carcasses: Essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries*, 24(10):6–15.

Chapin, F. S., Walker, B. H., Hobbs, R. J., Hooper, D. U., Lawton, J. H., Sala, O. E., and Tilman, D. (1997). Biotic control over the functioning of ecosystems. *Science*, 277(5325):500–504.

Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., and Diaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405(6783):234–242.

Clarke, A. (1993). Temperature And Extinction In The Sea - A Physiologists View. *Paleobiology*, 19(4):499–518.

Cohen, J. E., Beaver, R. A., Cousins, S. H., Deangelis, D. L., Goldwasser, L., Heong, K. L., Holt, R. D., Kohn, A. J., Lawton, J. H., Martinez, N., Omalley, R., Page, L. M., Patten, B. C., Pimm, S. L., Polis, G. A., Rejmanek, M., Schoener, T. W., Schoenly, K., Sprules, W. G., Teal, J. M., Ulanowicz, R. E., Warren, P. H., Wilbur, H. M., and Yodzis, P. (1993). Improving Food Webs. *Ecology*, 74(1):252–258.

Collares-Pereira, M. J., Martins, M. J., Pires, A. M., Geraldes, A. M., and Coelho, M. M. (1996). Feeding behaviour of Barbus bocagei assessed under a spatio-temporal approach. *Folia Zoologica*, 45(1):65–76.

Collins, P. T. (1992). Length Biomass Relationships for Terrestrial Gastropoda and Oligochaeta. *American Midland Naturalist*, 128(2):404–406.

Cooke, S. J. and Cowx, I. G. (2004). The role of recreational fishing in global fish crises. *Bioscience*, 54(9):857–859.

Cooper, S. D., Walde, S. J., and Peckarsky, B. L. (1990). Prey Exchange-rates and the Impact of Predators On Prey Populations In Streams. *Ecology*, 71(4):1503–1514.

Copp, G. H., Bianco, P. G., Bogutskaya, N. G., Eros, T., Falka, I., Ferreira, M. T., Fox, M. G., Freyhof, J., Gozlan, R. E., Grabowska, J., Kovac, V., Moreno-Amich, R., Naseka, A. M., Penaz, M., Povz, M., Przybylski, M., Robillard, M., Russell, I. C., Stakenas, S., Sumer, S., Vila-Gispert, A., and Wiesner, C. (2005a). To be, or not to be, a non-native freshwater fish? *Journal of Applied Ichthyology*, 21(4):242–262.

Copp, G. H., Garthwaite, R., and Gozlan, R. E. (2005b). Risk identification and assessment of non-native freshwater fishes: a summary of concepts and perspectives on protocols for the UK. *Journal of Applied Ichthyology*, 21(4):371–373.

Copp, G. H., Spathari, S., and Turmel, M. (2005c). Consistency of Diel behaviour and interactions of stream fishes and invertebrates during summer. *River Research and Applications*, 21(1):75–90.

Copp, G. H., Templeton, M., and Gozlan, R. E. (2007). Propagule pressure and the invasion risks of non-native freshwater fishes: a case study in England. *Journal Of Fish Biology*, 71:148–159.

Copp, G. H., Vilizzi, L., and Gozlan, R. E. (2010a). The demography of introduction pathways, propagule pressure and occurrences of non-native freshwater fish in

England. *Aquatic Conservation-marine and Freshwater Ecosystems*, 20(5):595–601.

Copp, G. H., Vilizzi, L., and Gozlan, R. E. (2010b). Fish movements: the introduction pathway for topmouth gudgeon Pseudorasbora parva and other non-native fishes in the UK. *Aquatic Conservation-marine and Freshwater Ecosystems*, 20(3):269–273.

Copp, G. H., Wesley, K. J., and Vilizzi, L. (2005d). Pathways of ornamental and aquarium fish introductions into urban ponds of Epping Forest (London, England): the human vector. *Journal of Applied Ichthyology*, 21(4):263–274.

Costanza, R., dArge, R., deGroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., ONeill, R. V., Paruelo, J., Raskin, R. G., Sutton, P., and vanden-Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature*, 387(6630):253–260.

Coutant, C. C. (1987). Thermal Preference - When Does An Asset Become A Liability. *Environmental Biology of Fishes*, 18(3):161–172.

Covich, A. P., Austen, M. C., Barlocher, F., Chauvet, E., Cardinale, B. J., Biles, C. L., Inchausti, P., Dangles, O., Solan, M., Gessner, M. O., Statzner, B., and Moss, B. (2004). The role of Biodiversity in the functioning of freshwater and marine benthic ecosystems. *Bioscience*, 54(8):767–775.

Creed, R. P. (2006). Predator transitions in stream communities: a model and evidence from field studies. *Journal of the North American Benthological Society*, 25(3):533–544.

Crisp, D. M. A. and Westlake, D. (1982). The temperatures of nine flowing waters in southern England. *Hydrobiologia*, 89:193–204.

Crowder, L. B. and Cooper, W. E. (1982). Habitat Structural Complexity and the Interaction Between Bluegills and Their Prey. *Ecology*, 63(6):1802–1813.

Cummins, K. W. (1974). Structure and Function of Stream Ecosystems. *Bioscience*, 24(11):631–641.

Cummins, K. W. and Wuycheck, J. C. (1971). *Caloric Equivalents for Investigations in Ecological Energetics*. Schweizerbart'sche Verlagsbuchhandling.

Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quinones, R. A., Shannon, L. J., and Verheye, H. M. (2000). Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *Ices Journal of Marine Science*, 57(3):603–618.

Daily, G. (1997). *Nature's services: societal dependence on natural ecosystems*. Island Press, Washington DC.

Dangles, O. and Guerold, F. (1999). Impact of headwater stream acidification on the trophic structure of macroinvertebrate communities. *International Review of Hydrobiology*, 84(3):287–297.

Daufresne, M., Roger, M. C., Capra, H., and Lamouroux, N. (2004). Long-term changes within the invertebrate and fish communities of the Upper Rhône River: effects of climatic factors. *Global Change Biology*, 10(1):124–140.

Davey, A. J. H. and Kelly, D. J. (2007). Fish community responses to drying disturbances in an intermittent stream: a landscape perspective. *Freshwater Biology*, 52(9):1719–1733.

Davic, R. D. (2003). Linking Keystone Species and Functional Groups: A New Operational Definition of the Keystone Species Concept. *Conservation Ecology [online]*, 7(1).

Davies, C. E. and Quill, V. (2004). *Freshwater fishes in Britain: the species and their distribution*. Harley Books.

Dawson, F. H. (1976). Organic contribution of stream edge forest litter fall to chalk stream ecosystem. *Oikos*, 27(1):13–18.

De Leo, G. A. and Levin, S. (1997). The multifaceted aspects of ecosystem integrity. *Conservation Ecology [online]*, 1(1):art. 3.

De Ruiter, P. C., Neutel, A.-M., and Moore, J. C. (1996). Energetics and stability in belowground food webs. *Food webs: Integration of patterns and dynamics*, pages 201–210.

De Ruiter, P. C., Neutel, A. M., and Moore, J. C. (1998). Biodiversity in soil ecosystems: the role of energy flow and community stability. *Applied Soil Ecology*, 10(3):217–228.

de Ruiter, P. C., Wolters, V., Moore, J. C., and Winemiller, K. O. (2005). Food web ecology: Playing Jenga and beyond. *Science*, 309(5731):68–+.

De Silva, S. S., Nguyen, T. T. T., Abery, N. W., and Amarasinghe, U. S. (2006). An evaluation of the role and impacts of alien finfish in Asian inland aquaculture. *Aquaculture Research*, 37(1):1–17.

DeAngelis, D. L. (1980). Energy-flow, Nutrient Cycling, and Ecosystem Resilience. *Ecology*, 61(4):764–771.

DeAngelis, D. L., Trexler, J. C., and Loftus, W. F. (2005). Life history trade-offs and community dynamics of small fishes in a seasonally pulsed wetland. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(4):781–790.

DeBruyn, A. M., McCann, K. S., and Rasmussen, J. B. (2004). Migration supports uneven consumer control in a sewage-enriched river food web. *Journal of Animal Ecology*, 73(4):737–746.

Declerck, S., Louette, G., De Bie, T., and De Meester, L. (2002). Patterns of diet overlap between populations of non-indigenous and native fishes in shallow ponds. *Journal of Fish Biology*, 61(5):1182–1197.

Dembski, S., Masson, G., Monnier, D., Wagner, P., and Phan, J. C. (2006). Consequences of elevated temperatures on life-history traits of an introduced fish, pumpkinseed Lepomis gibbosus. *Journal of Fish Biology*, 69(2):331–346.

DeRuiter, P., Wolters, V., and Moore, J. (2005). *Dynamic food webs: Multispecies assemblages, ecosystem development and environmental change*. Theoretocal Ecology Series. Academic Press.

Dewson, Z. S., James, A. B. W., and Death, R. G. (2007). A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society*, 26(3):401–415.

Dick, J. T. A., Montgomery, W. I., and Elwood, R. (1993). Replacement of the indigenous amphipod Gammarus duebeni celticus by the introduced G. pulex: differential cannibalism and mutual predation. *Journal of Animal Ecology*, 62:79–88.

Didham, R. K., Tylianakis, J. M., Hutchison, M. A., Ewers, R. M., and Gemmell, N. J. (2005). Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution*, 20(9):470–474.

Dodds, W. K. (2002). *Freshwater ecology Concepts and environmental Applications*. Academic Press.

Domaniewski, J. and Wheeler, A. (1996). The topmouth gudgeon has arrived. *Fish*, 43:40.

Downing, A. L. and Leibold, M. A. (2010). Species richness facilitates ecosystem resilience in aquatic food webs. *Freshwater Biology*, 55(10):2123–2137.

Duarte, C. M., Holmer, M., Olsen, Y., Soto, D., Marba, N., Guiu, J., Black, K., and Karakassis, I. (2009). Will the Oceans Help Feed Humanity? *Bioscience*, 59(11):967–976.

Duffy, J. E. (2002). Biodiversity and ecosystem function: the consumer connection. *Oikos*, 99(2):201–219.

Duffy, J. E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters*, 6(8):680–687.

Duffy, J. E. (2009). Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers In Ecology and the Environment*, 7(8):437–444.

Duffy, J. E., Cardinale, B. J., France, K. E., McIntyre, P. B., Thebault, E., and Loreau, M. (2007). The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, 10(6):522–538.

Duffy, J. E., Richardson, J. P., and Canuel, E. A. (2003). Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters*, 6(7):637–645.

Duggan, I. C., Rixon, C. A. M., and MacIsaac, H. J. (2006). Popularity and propagule pressure: Determinants of introduction and establishment of aquarium fish. *Biological Invasions*, 8(2):377–382.

Dunne, J. A., Williams, R. J., and Martinez, N. D. (2002a). Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America*, 99(20):12917–12922.

Dunne, J. A., Williams, R. J., and Martinez, N. D. (2002b). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 5(4):558–567.

Dunne, J. A., Williams, R. J., and Martinez, N. D. (2004). Network structure and robustness of marine food webs. *Marine Ecology-Progress Series*, 273:291–302.

Durance, I. and Ormerod, S. J. (2007). Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology*, 13(5):942–957.

Eby, L. A., Roach, W. J., Crowder, L. B., and Stanford, J. A. (2006). Effects of stocking-up freshwater food webs. *Trends in Ecology & Evolution*, 21(10):576–584.

Ehrlich, P. R., E. A. H. (1981). *Extinction: the causes and consequences of the disappearance of species*. Random House, New York.

Eklof, A. and Ebenman, B. (2006). Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology*, 75(1):239–246.

Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B., and Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers In Ecology and the Environment*, 1(9):488–494.

Elton, C. (1958). *The Ecology of Invasions by Animals and Plants*. Chapman & Hall, London.

Emmerson, M. C. and Raffaelli, D. (2004). Predator-prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, 73(3):399–409.

Emmerson, M.C., M. J. and Woodward, G. (2005). Body size, interaction strength and food web dynamics. In de Ruiter, P., Wolters, V., and Moore, J., editors, *Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development and Environmental Change*, pages 167–178. Academic Press, San Diego, California.

Englund, G. (1997). Importance of spatial scale and prey movements in predator caging experiments. *Ecology*, 78(8):2316–2325.

Faith, D. P., Minchin, P. R., and Belbin, L. (1987). Compositional Dissimilarity As A Robust Measure of Ecological Distance. *Vegetatio*, 69(1-3):57–68.

FAO (2008). The State of World Fisheries and Aquaculture. Technical report, FAO, Rome.

Fasham, M. J. R. (1977). Comparison of Nonmetric Multidimensional-scaling, Principal Components and Reciprocal Averaging For Ordination of Simulated Coenoclines, and Coenoplanes. *Ecology*, 58(3):551–561.

Fath, B. D. (2004). Network analysis applied to large-scale cyber-ecosystems. *Ecological Modelling*, 171(4):329–337.

Field, J. G., Clarke, K. R., and Warwick, R. M. (1982). A Practical Strategy For Analyzing Multispecies Distribution Patterns. *Marine Ecology-progress Series*, 8(1):37–52.

Finke, D. L. and Denno, R. F. (2004). Predator diversity dampens trophic cascades. *Nature*, 429(6990):407–410.

Folke, C. (2003). Freshwater for resilience: a shift in thinking. *Philosophical Transactions of the Royal Society of London Series B-biological Sciences*, 358(1440):2027–2036.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C. S. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology Evolution and Systematics*, 35:557–581.

Folke, C., Holling, C. S., and Perrings, C. (1996). Biological diversity, ecosystems, and the human scale. *Ecological Applications*, 6(4):1018–1024.

Franssen, N. R., Gido, K. B., and Propst, D. L. (2007). Flow regime affects availability of native and nonnative prey of an endangered predator. *Biological Conservation*, 138(3-4):330–340.

Fruget, J. F., Centofanti, M., Dessaix, J., Olivier, J. M., Druart, J. C., and Martinez, P. J. (2001). Temporal and spatial dynamics in large rivers: example of a long-term monitoring of the middle Rhone River. *Annales De Limnologie-international Journal of Limnology*, 37(3):237–251.

Fry, F. (1971). The effect of environmental factors on the physiology of fish. In Hoar, W. and Randal, D., editors, *Fish Physiology Volume VI: Environmental Relations and Behavior*, pages 1–98. Academic Press, New York.

FSBI (2007). Climate change and the fishes of Britain and Ireland: Briefing Paper 4.

Fussmann, G. F. and Heber, G. (2002). Food web complexity and chaotic population dynamics. *Ecology Letters*, 5(3):394–401.

Gamfeldt, L., Hillebrand, H., and Jonsson, P. R. (2008). Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology*, 89(5):1223–1231.

Garner, P., Clough, S., Griffiths, S. W., Deans, D., and Ibbotson, A. (1998). Use of shallow marginal habitat by Phoxinus phoxinus: a trade-off between temperature and food? *Journal of Fish Biology*, 52(3):600–609.

Gherardi, F., Bertolino, S., Bodon, M., Casellato, S., Cianfanelli, S., Ferraguti, M., Lori, E., Mura, G., Nocita, A., Riccardi, N., Rossetti, G., Rota, E., Scalera, R., Zerunian, S., and Tricarico, E. (2008). Animal xenodiversity in Italian inland waters: distribution, modes of arrival, and pathways. *Biological Invasions*, 10(4):435–454.

Gillespie, D. T. (2000). The chemical Langevin equation. *J. Chem. Phys.*, 113(1):297–306.

Gitay, H., Wilson, J. B., and Lee, W. G. (1996). Species redundancy: A redundant concept? *Journal of Ecology*, 84(1):121–124.

Gozlan, R. (2008a). Correspondence: When human understanding of fish invasion is blurred. *PLoS Biol*, 6:28.

Gozlan, R. E. (2008b). Introduction of non-native freshwater fish: is it all bad? *Fish and Fisheries*, 9(1):106–115.

Gozlan, R. E., Andreou, D., Asaeda, T., Beyer, K., Bouhadad, R., Burnard, D., Caiola, N., Cakic, P., Djikanovic, V., Esmaeili, H. R., Falka, I., Golicher, D., Harka, A., Jeney, G., Kovac, V., Musil, J., Nocita, A., Povz, M., Poulet, N., Virbickas, T., Wolter, C., Serhan Tarkan, A., Tricarico, E., Trichkova, T., Verreycken, H., Witkowski, A., Guang Zhang, C., Zweimueller, I., and Robert Britton, J. (2010a). Pan-continental invasion of Pseudorasbora parva: towards a better understanding of freshwater fish invasions. *Fish and Fisheries*, 11(4):315–340.

Gozlan, R. E., Britton, J. R., Cowx, I., and Copp, G. H. (2010b). Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology*, 76(4):751–786.

Gozlan, R. E., Pinder, A. C., and Shelley, J. (2002). Occurrence of the Asiatic

cyprinid Pseudorasbora parva in England. *Journal of Fish Biology*, 61(1):298–300.

Gozlan, R. E., St-Hilaire, S., Feist, S. W., Martin, P., and Kent, M. L. (2005). Biodiversity - Disease threat to European fish. *Nature*, 435(7045):1046–1046.

Gozlan, R. E., Whipps, C. M., Andreou, D., and Arkush, K. D. (2009). Identification of a rosette-like agent as Sphaerothecum destruens, a multi-host fish pathogen. *International Journal For Parasitology*, 39(10):1055–1058.

Green, D. G. and Sadedin, S. (2005). Interactions matter - complexity in landscapes and ecosystems. *Ecological Complexity*, 2(2):117–130.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86(6):902–910.

Grimm, N. B., Foster, D., Groffman, P., Grove, J. M., Hopkinson, C. S., Nadelhoffer, K. J., Pataki, D. E., and Peters, D. P. C. (2008). The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. *Frontiers In Ecology And The Environment*, 6(5):264–272.

Grimm, V. and Wissel, C. (1997). Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109(3):323–334.

Groombridge, B. and Jenkins, M. D. (2002). *World Atlas of Biodiversity Earth's Living Resources in the 21st Century*. University of California Press, Berkeley.

Guma'a, S. A. (1978). Effects Of Temperature On Development And Mortality Of Eggs Of Perch, Perca-Fluviatilis. *Freshwater Biology*, 8(3):221–227.

Gunderson, L. H. (2000). Ecological resilience - in theory and application. *Annual Review of Ecology and Systematics*, 31:425–439.

Gunderson, L. H. and Holling, C. S. (2002). *Panarchy: understanding transformations in human and natural systems*. Island Press.

Gurevitch, J. and Padilla, D. K. (2004). Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution*, 19(9):470–474.

Hall, R. O., Wallace, J. B., and Eggert, S. L. (2000). Organic matter flow in stream food webs with reduced detrital resource base. *Ecology*, 81(12):3445–3463.

Hall, S. R., Shurin, J. B., Diehl, S., and Nisbet, R. M. (2007). Food quality, nutrient limitation of secondary production, and the strength of trophic cascades. *Oikos*, 116(7):1128–1143.

Ham, S. F., Cooling, D. A., Hiley, P. D., Mcleish, P. R., Scorgie, H. R. A., and Berrie, A. D. (1982). Growth and Recession of Aquatic Macrophytes On A Shaded Section of the River Lambourn, England, From 1971 To 1980. *Freshwater Biology*, 12(1):1–15.

Ham, S. F., Wright, J. F., and Berrie, A. D. (1981). Growth and Recession of Aquatic Macrophytes On An Unshaded Section of the River Lambourn, England, From 1971 To 1976. *Freshwater Biology*, 11(4):381–390.

Hancock, R. S., Jones, J. W., and Shaw, R. (1976). Preliminary-report On Spawning Behavior and Nature of Sexual Selection In Barbel, Barbus-barbus (l). *Journal of Fish Biology*, 9(1):21–28.

Hanfling, B., Bolton, P., Harley, M., and Carvalho, G. R. (2005). A molecular approach to detect hybridisation between crucian carp (Carassius carassius) and non-indigenous carp species (Carassius spp. and Cyprinus carpio). *Freshwater Biology*, 50(3):403–417.

Hannah, L., Lovejoy, T. E., and Schneider, S. H. (2005). Biodiversity and Climate change in Context. In Lovejoy, T. E. and Hannah, L., editors, *Climate change and Biodiversity*, chapter 1, pages 3–14. Yale University Press.

Hastings, A. and Powell, T. (1991). Chaos in a 3-Species Food-Chain. *Ecology*, 72(3):896–903.

Hawkes, H. A. (1998). Origin and development of the Biological Monitoring Working Party score system. *Water Research*, 32(3):964–968.

He, X., Kitchell, J. F., Carpenter, S. R., Hodgson, J. R., Schindler, D. E., and Cottingham, K. L. (1993). Food-web Structure and Long-term Phosphorus Recycling - A Simulation-model Evaluation. *Transactions of the American Fisheries Society*, 122(5):773–783.

Hecky, R. E. and Hesslein, R. H. (1995). Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society*, 14(4):631–653.

Hector, A. and Bagchi, R. (2007). Biodiversity and ecosystem multifunctionality. *Nature*, 448(7150):188–U6.

Hickley, J. and North, E. (1983). Zander threaten the Severn: True or false? In *The 3rd British Freshwater Fish. Conference*. Liverpool University.

Hickley, P. (1986). Invasion By Zander and the Management of Fish Stocks. *Philosophical Transactions of the Royal Society of London Series B-biological Sciences*, 314(1167):571–582.

Hickley, P. and Chare, S. (2004). Fisheries for non-native species in England and Wales: angling or the environment? *Fisheries Management and Ecology*, 11(3-4):203–212.

Hickling, R., Roy, D. B., Hill, J. K., Fox, R., and Thomas, C. D. (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, 12(3):450–455.

Hoekman, D. (2010). Turning up the heat: Temperature influences the relative importance of top-down and bottom-up effects. *Ecology*, 91(10):2819–2825.

Holcik, J. (1991). Fish Introductions In Europe With Particular Reference To Its Central and Eastern Part. *Canadian Journal of Fisheries and Aquatic Sciences*, 48:13–23.

Holling, C. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4:1–23.

Holmes, N. T. H. (2006). The importance of long-term data sets in science and river management. *Aquatic Conservation-marine and Freshwater Ecosystems*, 16(4):329–333.

Holmlund, C. M. and Hammer, M. (1999). Ecosystem services generated by fish populations. *Ecological Economics*, 29(2):253–268.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A. J., Vandermeer, J., and Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75(1):3–35.

Hooper, D. U. and Dukes, J. S. (2004). Overyielding among plant functional groups in a long-term experiment. *Ecology Letters*, 7(2):95–105.

Horton, P. A. (1961). The Bionomics of Brown Trout in a Dartmoor Stream. *Journal of Animal Ecology*, 30(2):311–338.

Hughes, T. P. (1994). Catastrophes, Phase-shifts, and Large-scale Degradation of A Caribbean Coral-reef. *Science*, 265(5178):1547–1551.

Hurlbert, S. H. (1997). Functional importance vs keystoneness: Reformulating some questions in theoretical biocenology. *Australian Journal of Ecology*, 22(4):369–382.

Huryn, A. D. (1998). Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. *Oecologia*, 115(1-2):173–183.

Huston, M. A. (1997). Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110(4):449–460.

Hutchinson, G. E. (1959). Homage To Santa-rosalia Or Why Are There So Many Kinds of Animals. *American Naturalist*, 93(870):145–159.

Hynes, H. B. N. (1983). Groundwater and Stream Ecology. *Hydrobiologia*, 100:93–99.

Hyslop, E. J. (1980). Stomach Contents Analysis - a Review of Methods and Their Application. *J. Fish Biol.*, 17(4):411–429.

Hyslop, E. J. (1982). The Feeding-Habits of O + Stone Loach, Noemacheilus-Barbatulus (L), and Bullhead, Cottus-Gobio L. *Journal of Fish Biology*, 21(2):187–196.

Ings, T. C., Montoya, J. M., Bascompte, J., Bluthgen, N., Brown, L., Dormann, C. F., Edwards, F., Figueroa, D., Jacob, U., Jones, J. I., Lauridsen, R. B., Ledger, M. E., Lewis, H. M., Olesen, J. M., van Veen, F. J. F., Warren, P. H., and Woodward, G. (2009). Ecological networks - beyond food webs. *Journal Of Animal Ecology*, 78(1):253–269.

IPCC (2007). IPCC Fourth Assessment Report: Climate Change. Technical report, Intergovernmental Panel on Climate Change.

Jaksic, F. M. (1981). Abuse and Misuse of the Term Guild In Ecological-studies. *Oikos*, 37(3):397–400.

Jaksic, F. M. and Medel, R. G. (1990). Objective Recognition of Guilds - Testing For Statistically Significant Species Clusters. *Oecologia*, 82(1):87–92.

Jang, M. H., Joo, G. J., and Lucas, M. C. (2006). Diet of introduced largemouth bass in Korean rivers and potential interactions with native fishes. *Ecology of Freshwater Fish*, 15(3):315–320.

Jenkins, B., Kitching, R. L., and Pimm, S. L. (1992). Productivity, Disturbance and Food Web Structure At A Local Spatial Scale In Experimental Container Habitats. *Oikos*, 65(2):249–255.

Jenkins, G., Perry, M., and Prior, M. (2008). The climate of the United Kingdom and recent trends. Technical report, Met Office Hadley Centre, Exeter, UK, Exeter, UK.

Johnson, A. C., Acreman, M. C., Dunbar, M. J., Feist, S. W., Giacomello, A. M., Gozlan, R. E., Hinsley, S. A., Ibbotson, A. T., Jarvie, H. P., Jones, J. I., Longshaw, M., Maberly, S. C., Marsh, T. J., Neal, C., Newman, J. R., Nunn, M. A., Pickup, R. W., Reynard, N. S., Sullivan, C. A., Sumpter, J. P., and Williams, R. J. (2009a). The British river of the future: How climate change and human activity might affect two contrasting river ecosystems in England. *Science of the Total Environment*, 407(17):4787–4798.

Johnson, G. A., Niquil, N., Asmus, H., Bacher, C., Asmus, R., and Baird, D. (2009b). The effects of aggregation on the performance of the inverse method and indicators of network analysis. *Ecological Modelling*, 220(23):3448–3464.

Jonsson, M., Dangles, O., Malmqvist, B., and Guerold, F. (2002). Simulating species loss following perturbation: assessing the effects on process rates. *Proceedings of the Royal Society of London Series B-biological Sciences*, 269(1495):1047–1052.

Jonsson, T. and Ebenman, B. (1998). Effects of predator-prey body size ratios on the stability of food chains. *Journal of Theoretical Biology*, 193(3):407–417.

Jordan, F. (2009). Keystone species and food webs. *Philosophical Transactions of the Royal Society B-biological Sciences*, 364(1524):1733–1741.

Jordan, F., Liu, W. C., and Wyatt, T. (2005). Topological constraints on the dynamics of wasp-waist ecosystems. *Journal of Marine Systems*, 57(3-4):250–263.

Jordan, F., Okey, T. A., Bauere, B., and Libralato, S. (2008). Identifying important species: Linking structure and function in ecological networks. *Ecological Modelling*, 216(1):75–80.

Jorgensen, S. E. (2007). Ecological network theory. *Ecological Modelling*, 208(1):1–2.

Jost, L. (2006). Entropy and diversity. *Oikos*, 113(2):363–375.

Karr, J. R. and Dudley, D. R. (1981). Ecological Perspective On Water-Quality Goals. *Environmental Management*, 5(1):55–68.

Kay, J. J. (2000). Ecosystems as Self-Organizing Holarchic Open Systems: Narratives and the Second Law of Thermodynamics. In Jorgensen, S. E. and Mueller, F., editors, *Handbook of Ecosystem Theories and Management*, pages 135–160. CRC Press - Lewis Publishers.

Kazanci, C. (2007). EcoNet: A new software for ecological modeling, simulation and network analysis. *Ecological Modelling*, 208(1):3–8.

Keller, R. P. and Lodge, D. M. (2007). Species invasions from commerce in live aquatic organisms: Problems and possible solutions. *Bioscience*, 57(5):428–436.

Kenkel, N. C. and Orloci, L. (1986). Applying Metric and Nonmetric Multidimensional-scaling To Ecological-studies - Some New Results. *Ecology*, 67(4):919–928.

King, A. W. and Pimm, S. L. (1983). Complexity, Diversity, and Stability - A Reconciliation of Theoretical and Empirical Results. *American Naturalist*, 122(2):229–239.

Klee, C. A. (1981). An assessment of the contribution made by zander to the decline of fisheries in the lower Great Ouse area. In *The 2nd British Freshwater Fish. Conference*. Liverpool University.

Knight, C. M. (2006). *Utilisation of Off-River Habitats by Lowland River Fishes*. PhD thesis, University of Durham School of Biological and Biomedical Sciences .

Knight, T. M., McCoy, M. W., Chase, J. M., McCoy, K. A., and Holt, R. D. (2005). Trophic cascades across ecosystems. *Nature*, 437(7060):880–883.

Knowlton, N. (2001). The future of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*, 98(10):5419–5425.

Koel, T. M., Bigelow, P. E., Doepke, P. D., Ertel, B. D., and Mahony, D. L. (2005). Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. *Fisheries*, 30(11):10–19.

Kolar, C. S. and Lodge, D. M. (2002). Ecological predictions and risk assessment for alien fishes in North America. *Science*, 298(5596):1233–1236.

Kopp, D., Cucherousset, J., Syvaranta, J., Martino, A., Cereghino, R., and Santoul, F. (2009). Trophic ecology of the pikeperch (Sander lucioperca) in its introduced areas: a stable isotope approach in southwestern France. *Comptes Rendus Biologies*, 332(8):741–746.

Kottelat, M. and Freyhof, J. (2007). *Handbook of European freshwater fishes*. Publications Kottelat, Cornol, Switzerland.

Kramer, D., Rangeley, R., and Chapman, L. (1997). Habitat selection: patterns of spatial distribution from behavioural decisions. In Godin, G., editor, *Behavioural Ecology of Teleost Fishes*, pages 37–80. Oxford University Press, Oxford.

Kruskal, J. B. (1964a). Multidimensional-scaling By Optimizing Goodness of Fit To A Nonmetric Hypothesis. *Psychometrika*, 29(1):1–27.

Kruskal, J. B. (1964b). Nonmetric Multidimensional-scaling - A Numerical-method. *Psychometrika*, 29(2):115–129.

Kruskal, J. B. and Wish, M. (1978). *Multidimensional Scaling, Sage University Paper series on Quantitative Application in the Social Sciences, 07-011. Beverly Hills and London: Sage Publications.* Sage University Paper series on Quantitative Application in the Social Sciences. Sage Publications, Beverly Hills. CA.

Kumar, R. and Hwang, J. S. (2006). Larvicidal efficiency of aquatic predators: A perspective for mosquito biocontrol. *Zoological Studies*, 45(4):447–466.

Körner, C. (1993). Scaling from species to vegetation: the usefulness of functional groups. In Schulze, E. D. and Mooney, H. A., editors, *Biodiversity and ecosystem function*, pages 117–140. Springer Verlag.

Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, 48(7):1161–1172.

Lal, R. (2007). Anthropogenic influences on world soils and implications to global food security. *Advances In Agronomy, Vol 93*, 93:69–93.

Lamont, B. (1992). In *Biodiversity in Mediterranean ecosystems of Australia*, pages 95–127–. Surrey Beatty, Chipping Norton, Australia.

Lampert, W. and Sommer, U. (1999). *Limnooekologie*. Thieme.

Lappalainen, J., Dörner, H., and Wysujack, K. (2003). Reproduction biology of pikeperch (Sander lucioperca (L.)) - a review. *Ecology of Freshwater Fish*, 12(2):95–106.

Larsen, T. H., Williams, N. M., and Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, 8(5):538–547.

Laska, M. S. and Wootton, J. T. (1998). Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology*, 79(2):461–476.

Lawton, J. H., B. V. K. (1993). Redundancy in ecosystems. In Schulze, E. D. and Mooney, H. A., editors, *Bioversity and ecosystem function.*, pages 255–270. Springer Verlag, New York.

Lawton, J. and May, R. (1996). *Extinction Rates*. Oxford University Press.

Le Morvan, C., Troutaud, D., and Deschaux, P. (1998). Differential effects of temperature on specific and nonspecific immune defences in fish. *Journal of Experimental Biology*, 201(2):165–168.

Leah, R. T. and Kell, L. (1985). The impact of introducing zander to a British Fishery. In *The 4th British Freshwater Fish. Conference*. Liverpool University.

Lecerf, A. and Richardson, J. S. (2010). Biodiversity-ecosystem Function Research: Insights Gained From Streams. *River Research and Applications*, 26(1):45–54.

Leprieur, F., Brosse, S., Garcia-Berthou, E., Oberdorff, T., Olden, J. D., and Townsend, C. R. (2009). Scientific uncertainty and the assessment of risks posed by non-native freshwater fishes. *Fish and Fisheries*, 10(1):88–97.

Lewis, V. (2004). The management of freshwater fisheries. Guidance note, The National Trust.

Linfield, R. and Rickards, R. (1979). The Zander in Perspective. *Aquaculture Research*, 10(1):1–16.

Linfield, R. S. J. (1982). The impact of zander Stizostedion lucioperca (L) in the United Kingdom and future management of affected fisheries in the Anglian region. In *EIFAC Symposium*, Hungary.

Loeuille, N. and Loreau, M. (2006). Evolution of body size in food webs: does the energetic equivalence rule hold? *Ecology Letters*, 9(2):171–178.

Loreau, M. and Behera, N. (1999). Phenotypic diversity and stability of ecosystem processes. *Theoretical Population Biology*, 56(1):29–47.

Loreau, M. and Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412(6842):72–76.

Loreau, M., Mouquet, N., and Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, 100(22):12765–12770.

Lotka, A. J. (1925). *Elements of physical biology*. Williams and Wilkins, Baltimore.

Lucas, M. C. and Batley, E. (1996). Seasonal movements and behaviour of adult barbel Barbus barbus, a riverine cyprinid fish: Implications for river management. *Journal of Applied Ecology*, 33(6):1345–1358.

Luvall, J. C., Lieberman, D., Lieberman, M., Hartshorn, G. S., and Peralta, R. (1990). Estimation of Tropical Forest Canopy Temperatures, Thermal Response Numbers, and Evapotranspiration Using An Aircraft-based Thermal Sensor. *Photogrammetric Engineering and Remote Sensing*, 56(10):1393–1401.

Lyons, K. G., Brigham, C. A., Traut, B. H., and Schwartz, M. W. (2005). Rare species and ecosystem functioning. *Conservation Biology*, 19(4):1019–1024.

MacArthur, R. (1955). Fluctuations Of Animal Populations, And A Measure Of Community Stability. *Ecology*, 36(3):533–536.

Magurran, A. E. (2004). *Measuring biological diversity*. Blackwell Publishing.

Maitland, P. and Campbell, R. (1992). *Freshwater fishes of the British Isles*. Harper-Collins Publishers, London.

Maitland, P. S. (1965). The Feeding Relationships of Salmon, Trout, Minnows, Stone Loach and 3-Spined Sticklebacks in the River Endrick, Scotland. *J. Anim. Ecol.*, 34(1):109–133.

Malmqvist, B. and Rundle, S. (2002). Threats to the running water ecosystems of the world. *Environmental Conservation*, 29(2):134–153.

Mann, R. H. K. (1971). Populations, Growth and Production of Fish in 4 Small Streams in Southern England. *J. Anim. Ecol.*, 40(1):155.

Mann, R. H. K. (1974). Observations On Age, Growth, Reproduction And Food Of Dace, Leuciscus-Leuciscus (L) In 2 Rivers In Southern England. *Journal Of Fish Biology*, 6(3):237–253.

Mann, R. H. K. (1976a). Observations on Age, Growth, Reproduction and Food of Chub Squalius-Cephalus L in River Stour, Dorset. *Journal of Fish Biology*, 8(3):265.

Mann, R. H. K. (1976b). Observations on Age, Growth, Reproduction and Food of Pike Esox-Lucius-(L.) in 2 Rivers in Southern England. *Journal of Fish Biology*, 8(2):179–197.

Mann, R. H. K. (1980a). The Growth and Reproductive Strategy of the Gudgeon, Gobio-Gobio (L), in 2 Hard-Water Rivers in Southern England. *Journal of Fish Biology*, 17(2):163–176.

Mann, R. H. K. (1980b). The Numbers and Production of Pike (Esox-Lucius) in 2 Dorset Rivers. *Journal of Animal Ecology*, 49(3):899–915.

Mann, R. H. K. (1982). The Annual Food-Consumption and Prey Preferences of Pike (Esox-Lucius) in the River Frome, Dorset. *Journal of Animal Ecology*, 51(1):81–95.

Mann, R. H. K. and Bass, J. A. B. (1997). The critical water velocities of larval roach (Rutilus rutilus) and dace (Leuciscus leuciscus) and implications for river management. *Regulated Rivers: Research & Management*, 13(3):295–301.

Mann, R. H. K. and Blackburn, J. H. (1991). The Biology of the Eel Anguilla-Anguilla (L) in an English Chalk Stream and Interactions with Juvenile Trout Salmo-Trutta L and Salmon Salmo-Salar L. *Hydrobiologia*, 218(1):65–76.

Mann, R. H. K., Blackburn, J. H., and Beaumont, W. R. C. (1989). The Ecology of Brown Trout Salmo-Trutta in English Chalk Streams. *Freshwater Biology*, 21(1):57–70.

Mann, R. H. K. and Orr, D. R. O. (1969). A Preliminary Study of Feeding Relationships of Fish in a Hard-Water and a Soft-Water Stream in Southern England. *J. Fish Biol.*, 1(1):31.

Marchetti, M. P. and Moyle, P. B. (2001). Effects of flow regime on fish assemblages in a regulated california stream. *Ecological Applications*, 11(2):530–539.

Marcogliese, D. J. (2008). The impact of climate change on the parasites and infectious diseases of aquatic animals. *Revue Scientifique Et Technique-Office International Des Epizooties*, 27(2):467–484.

Margalef, R. (1972). Homage to Evelyn Hutchinson or why there is an upper limit to diversity. *Transactions Connecticut Academy of Arts and Sciences*, 44:211–235.

Marker, A. F. H. (1976). Benthic Algae of Some Streams In Southern England .2. Primary Production of Epilithon In A Small Chalk-stream. *Journal of Ecology*, 64(1):359–373.

Martinez, N. D., Williams, R. J., and Dunne, J. A. (2006). Diversity, complexity,

and persistence in large model ecosystems. *Ecological Networks: Linking Structure to Dynamics in Food Webs*, pages 163–185.

May, R. M. (1972). Will A Large Complex System Be Stable. *Nature*, 238(5364):413–414.

May, R. M. (1973). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NY, 2 edition.

McCann, K. and Hastings, A. (1997). Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society of London Series B-biological Sciences*, 264(1385):1249–1254.

McCann, K., Hastings, A., and Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395(6704):794–798.

McCann, K. S. (2000). The diversity-stability debate. *Nature*, 405(6783):228–233–.

McCoy, R. (1994). *The best of Deming*. Statistical Process Control Press, Knoxville, Tennessee, USA.

McGradySteed, J., Harris, P. M., and Morin, P. J. (1997). Biodiversity regulates ecosystem predictability. *Nature*, 390(6656):162–165.

McIntosh, A. R. and Townsend, C. (1995). Impacts of an introduced predatory fish on mayfly grazing in New Zealand streams. *Limnology and Oceanography*, 40:1508–1512.

Meissner, K. and Muotka, T. (2006). The role of trout in stream food webs: integrating evidence from field surveys and experiments. *Journal of Animal Ecology*, 75(2):421–433.

Miller, S. A. and Crowl, T. A. (2006). Effects of common carp (Cyprinus carpio) on macrophytes and invertebrate communities in a shallow lake. *Freshwater Biology*, 51(1):85–94.

Mills, L. S., Soule, M. E., and Doak, D. F. (1993). The Keystone-Species Concept in Ecology and Conservation. *Bioscience*, 43(4):219–224.

Minchin, P. R. (1987). An Evaluation of the Relative Robustness of Techniques For Ecological Ordination. *Vegetatio*, 69(1-3):89–107.

Mion, J. B., Stein, R. A., and Marschall, E. A. (1998). River discharge drives survival of larval walleye. *Ecological Applications*, 8(1):88–103.

Montoya, J. M., Rodriguez, M. A., and Hawkins, B. A. (2003). Food web complexity and higher-level ecosystem services. *Ecology Letters*, 6(7):587–593.

Montoya, J. M. and Sole, R. V. (2002). Small world patterns in food webs. *Journal of Theoretical Biology*, 214(3):405–412.

Montoya, J. M. and Sole, R. V. (2003). Topological properties of food webs: from real data to community assembly models. *Oikos*, 102(3):614–622.

Montoya, J. M. and Yvon-Durocher, G. (2007). Ecological networks: Information theory meets Darwin's entangled bank. *Current Biology*, 17(4):R128–R130.

Moore, J. C., Berlow, E. L., Coleman, D. C., de Ruiter, P. C., Dong, Q., Hastings, A., Johnson, N. C., McCann, K. S., Melville, K., Morin, P. J., Nadelhoffer, K., Rosemond, A. D., Post, D. M., Sabo, J. L., Scow, K. M., Vanni, M. J., and Wall, D. H. (2004). Detritus, trophic dynamics and biodiversity. *Ecology Letters*, 7(7):584–600.

Morais, P. (2008). Review on the major ecosystem impacts caused by damming and watershed development in an Iberian basin (SW-Europe): focus on the Guadiana estuary. *Annales De Limnologie-International Journal Of Limnology*, 44(2):105–117.

Mugisha, J. Y. T. and Ddumba, H. (2007). Modelling the effect of Nile perch predation and harvesting on fisheries dynamics of Lake Victoria. *African Journal of Ecology*, 45(2):149–155.

Mulholland, P. J., Best, G. R., Coutant, C. C., Hornberger, G. M., Meyer, J. L., Robinson, P. J., Stenberg, J. R., Turner, R. E., VeraHerrera, F., and Wetzel, R. G. (1997). Effects of climate change on freshwater ecosystems of the south-eastern

United States and the Gulf Coast of Mexico. *Hydrological Processes*, 11(8):949–970.

Muus, B. and Dahlström, P. (1968). *Süßwasserfische*. BLV Verlagsgesellschaft, München.

Naeem, S. (1998). Species redundancy and ecosystem reliability. *Conservation Biology*, 12(1):39–45.

Naeem, S. and Li, S. B. (1997). Biodiversity enhances ecosystem reliability. *Nature*, 390(6659):507–509.

Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H., and Woodfin, R. M. (1995). Biodiversity and ecosystem functioning: empirical evidence from experimental microcosms. *Philosophical Transactions of the Royal Society, London*, 347:249–262.

Nakazawa, T., Ishida, N., Kato, M., and Yamamura, N. (2007). Larger body size with higher predation rate. *Ecology of Freshwater Fish*, 16(3):362–372.

Neutel, A. M., Heesterbeek, J. A. P., and de Ruiter, P. C. (2002). Stability in real food webs: Weak links in long loops. *Science*, 296(5570):1120–1123.

Newman, R. M. (1991). Herbivory and Detritivory On Fresh-water Macrophytes By Invertebrates - A Review. *Journal of the North American Benthological Society*, 10(2):89–114.

Nicolis, G., P. I. (1977). *Self-Organization in Non-Equilibrium Systems*. Wiley-Interscience.

Nilsson, C. and Renofalt, B. M. (2008). Linking Flow Regime and Water Quality in Rivers: a Challenge to Adaptive Catchment Management. *Ecology And Society*, 13(2).

Nilsson, E., Olsson, K., Persson, A., Nystrom, P., Svensson, G., and Nilsson, U. (2008). Effects of stream predator richness on the prey community and ecosystem attributes. *Oecologia*, 157(4):641–651.

Novikov, N., Sokolovsky, A., Sokolovskaya, T., and Yakovlev, Y. (2002). *The fishes of Primorye*. Far Eastern State Tech. Fish. Univ., Vladivostok.

NRA (1994). National Angling Survey. HMSO Publications. NRA (National Rivers Authority).

Nunn, A. D., Harvey, J. P., and Cowx, I. G. (2007). The food and feeding relationships of larval and 0+year juvenile fishes in lowland rivers and connected waterbodies. I. Ontogenetic shifts and interspecific diet similarity. *Journal of Fish Biology*, 70(3):726–742.

Nystrom, P. and McIntosh, A. R. (2003). Are impacts of an exotic predator on a stream food web influenced by disturbance history? *Oecologia*, 136(2):279–288.

Nystrom, P., McIntosh, A. R., and Winterbourn, M. J. (2003). Top-down and bottom-up processes in grassland and forested streams. *Oecologia*, 136(4):596–608.

O' Neill, R. V. (2001). Is it time to bury the ecosystem concept? (With full military honors of course!). *Ecology*, 82(12):3275–3284.

Ogutuohwayo, R. and Hecky, R. E. (1991). Fish Introductions In Africa and Some of Their Implications. *Canadian Journal of Fisheries and Aquatic Sciences*, 48:8–12.

O'Neill, R. V. (1976). Ecosystem Persistence and Heterotrophic Regulation. *Ecology*, 57(6):1244–1253.

Oscoz, J., Leunda, P. M., Miranda, R., and Escala, M. C. (2006). Summer feeding relationships of the co-occurring Phoxinus phoxinus and Gobio lozanoi (Cyprinidae) in an Iberian river. *FOLIA ZOOLOGICA*, 55(4):418–432.

Ostfeld, R. S. and LoGiudice, K. (2003). Community disassembly, biodiversity loss, and the erosion of an ecosystem service. *Ecology*, 84(6):1421–1427.

Otto, S. B., Rall, B. C., and Brose, U. (2007). Allometric degree distributions facilitate food-web stability. *Nature*, 450(7173):1226–U7.

Pacala, S. and Tilman, D. (2002). The transition from sampling to complementarity. In Kinzig, A., Pacala, S., and Tilman, D., editors, *The functional consequences of biodiversity. Empirical progress and theoretical extensions*. Princeton University Press, Princeton, NJ.

Pace, M. L., Cole, J. J., Carpenter, S. R., and Kitchell, J. F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution*, 14(12):483–488.

Paine, R. T. (1966). Food Web Complexity and Species Diversity. *The American Naturalist*, 100(910):65–75.

Paine, R. T. (1969a). A Note on Trophic Complexity and Community Stability. *The American Naturalist*, 103(929):91.

Paine, R. T. (1969b). Pisaster-Tegula Interaction - Prey Patches, Predator Food Preference, and Intertidal Community Structure. *Ecology*, 50(6):950.

Paine, R. T. (1995). A Conversation on Refining the Concept of Keystone Species. *Conservation Biology*, 9(4):962–964.

Pauly, D. and Pullin, R. S. V. (1988). Hatching Time In Spherical, Pelagic, Marine Fish Eggs In Response To Temperature And Egg Size. *Environmental Biology Of Fishes*, 22(4):261–271.

Pelicice, F. M. and Agostinho, A. A. (2009). Fish fauna destruction after the introduction of a non-native predator (Cichla kelberi) in a Neotropical reservoir. *Biological Invasions*, 11(8):1789–1801.

Perkins, D. M., Reiss, J., Yvon-Durocher, G., and Woodward, G. (2010). Global change and food webs in running waters. *Hydrobiologia*, 657(1):181–198.

Persson, L. (1986). Temperature-induced Shift In Foraging Ability In 2 Fish Species, Roach (rutilus-rutilus) and Perch (perca-fluviatilis) - Implications For Coexistence Between Poikilotherms. *Journal of Animal Ecology*, 55(3):829–839.

Petchey, O. L., Beckerman, A. P., Riede, J. O., and Warren, P. H. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences of the United States of America*, 105(11):4191–4196.

Petchey, O. L., Downing, A. L., Mittelbach, G. G., Persson, L., Steiner, C. F., Warren, P. H., and Woodward, G. (2004). Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos*, 104(3):467–478.

Petchey, O. L. and Gaston, K. J. (2002a). Extinction and the loss of functional diversity. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 269(1501):1721–1727.

Petchey, O. L. and Gaston, K. J. (2002b). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5(3):402–411.

Petchey, O. L., McPhearson, P. T., Casey, T. M., and Morin, P. J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, 402(6757):69–72.

Peters, R. (1983). *The Ecological Implications Of Body Size*. Cambridge University Press.

Pianka, E. R. (1980). Guild Structure In Desert Lizards. *Oikos*, 35(2):194–201.

Pilcher, M. W., Copp, G. H., and Szomolai, V. (2004). A comparison of adjacent natural and channelised strectches of a lowland river. *Biologia*, 59(5):669–673.

Pimm, S. L. (1980). Food Web Design and the Effect of Species Deletion. *Oikos*, 35(2):139–149.

Pimm, S. L. (1982). *Food Webs*. Univ Chicago Press.

Pimm, S. L. (1984). The Complexity and Stability of Ecosystems. *Nature*, 307(5949):321–326.

Pimm, S. L. and Lawton, J. H. (1978). Feeding On More Than One Trophic Level. *Nature*, 275(5680):542–544.

Pinder, A. C. and Gozlan, R. E. (2003). Sunbleak and Topmouth Gudgeon: Two New Additions to Britains Freshwater Fishes. *British Wildlife*, 15(2):77–83.

Pinder, A. C., Gozlan, R. E., and Britton, J. R. (2005). Dispersal of the invasive topmouth gudgeon, Pseudorasbora parva in the UK: a vector for an emergent infectious disease. *Fisheries Management and Ecology*, 12(6):411–414.

Pinder, L. C. V. (1992). Biology of Epiphytic Chironomidae (diptera, Nematocera) In Chalk Streams. *Hydrobiologia*, 248(1):39–51.

Pinnegar, J. K., Blanchard, J. L., Mackinson, S., Scott, R. D., and Duplisea, D. E. (2005). Aggregation and removal of weak-links in food-web models: system stability and recovery from disturbance. *Ecological Modelling*, 184(2-4):229–248.

Piraino, S., Fanelli, G., and Boero, F. (2002). Variability of species' roles in marine communities: change of paradigms for conservation priorities. *Marine Biology*, 140(5):1067–1074.

Planque, B. and Fredou, T. (1999). Temperature and the recruitment of Atlantic cod (Gadus morhua). *Canadian Journal Of Fisheries And Aquatic Sciences*, 56(11):2069–2077.

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., Sparks, R. E., and Stromberg, J. C. (1997). The natural flow regime. *Bioscience*, 47(11):769–784.

Poff, N. L., Brinson, M. M., and Day, J. j. (2002). *Aquatic ecosystems and global climate change*. Arlington.

Poff, N. L. and Hart, D. D. (2002). How dams vary and why it matters for the emerging science of dam removal. *Bioscience*, 52(8):659–668.

Poff, N. L. and Ward, J. V. (1989). Implications of Streamflow Variability and Predictability for Lotic Community Structure - a Regional-Analysis of Streamflow Patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, 46(10):1805–1818.

Poff, N. L. and Zimmerman, J. K. H. (2010). Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology*, 55(1):194–205.

Polis, G. A. (1999). Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*, 86(1):3–15.

Polis, G. A., Holt, R. D., Menge, B. A., and Winemiller, K. O. (1996). Time, space, and life history: Influences on food webs. In Polis, G. A. and Winemiller, K. O., editors, *Food webs: Integration of patterns and dynamics*, pages 435–460. Chapman and Hall, New York.

Polis, G. A. and Hurd, S. D. (1996a). Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: Examples from the ocean-land interface. In Polis, G. A. and Winemiller, K. O., editors, *Food webs: Integration of patterns and dynamics*, pages 435–460. Chapman and Hall, New York.

Polis, G. A. and Hurd, S. D. (1996b). Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist*, 147(3):396–423.

Polis, G. A., Sears, A. L. W., Huxel, G. R., Strong, D. R., and Maron, J. (2000). When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution*, 15(11):473–475.

Polley, H. W., Wilsey, B. J., and Derner, J. D. (2007). Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos*, 116(12):2044–2052.

Pont, D., Hugueny, B., and Oberdorff, T. (2005). Modelling habitat requirement of European fishes: do species have similar responses to local and regional environmental constraints? *Canadian Journal of Fisheries and Aquatic Sciences*, 62(1):163–173.

Post, D. M., Conners, M. E., and Goldberg, D. S. (2000). Prey preference by a top predator and the stability of linked food chains. *Ecology*, 81(1):8–14.

Post, D. M., Doyle, M. W., Sabo, J. L., and Finlay, J. C. (2007). The problem of boundaries in defining ecosystems: A potential landmine for uniting geomorphology and ecology.

Power, M. E. (1990). Effects of Fish in River Food Webs. *Science*, 250(4982):811–814.

Power, m. e. (1992). Top-down and Bottom-up Forces In Food Webs - Do Plants Have Primacy. *Ecology*, 73(3):733–746.

Power, M. E. (2006). Environmental controls on food web regimes: A fluvial perspective. *Progress In Oceanography*, 68(2-4):125–133.

Power, M. E. and Mills, L. S. (1995). The Keystone cops meet in Hilo. *Trends in Ecology & Evolution*, 10(5):182–184.

Power, M. E., Parker, M. S., and Dietrich, W. E. (2008). Seasonal reassembly of a river food web: Floods, droughts, and impacts of fish. *Ecological Monographs*, 78(2):263–282.

Power, M. E., Sun, A., Parker, G., Dietrich, W. E., and Wootton, J. T. (1995). Hydraulic Food-Chain Models. *Bioscience*, 45(3):159–167.

Power, M. E. and Tilman, D. (1996). Challenges in the quest for keystones. *Bioscience*, 46(8):609.

Prigogine, I. (1955). *Thermodynamics of Irreversible Processes*. John Wiley, New York.

Quist, M. and Yona, G. (2004). Distributional scaling: An algorithm for structure-preserving embedding of metric and nonmetric spaces. *Journal of Machine Learning Research*, 5:399–420J.

Raffaelli, D. (2004). How extinction patterns affect ecosystems. *Science*, 306(5699):1141–1142.

Rahel, F. J. (2007). Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. *Freshwater Biology*, 52(4):696–710.

Rahel, F. J. and Hubert, W. A. (1991). Fish Assemblages and Habitat Gradients In A Rocky-mountain Great-plains Stream - Biotic Zonation and Additive Patterns of Community Change. *Transactions of the American Fisheries Society*, 120(3):319–332.

Rall, B. C., Guill, C., and Brose, U. (2008). Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos*, 117(2):202–213.

Regier, H. A., Holmes, J. A., and Pauly, D. (1990). Influence Of Temperature-Changes On Aquatic Ecosystems - An Interpretation Of Empirical-Data. *Transactions of the American Fisheries Society*, 119(2):374–389.

Reiss, J., Bridle, J. R., Montoya, J. M., and Woodward, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends In Ecology & Evolution*, 24(9):505–514.

Resh, V. H., Brown, A. V., Covich, A. P., Gurtz, M. E., Li, H. W., Minshall, G. W., Reice, S. R., Sheldon, A. L., Wallace, J. B., and Wissmar, R. C. (1988). The Role of Disturbance in Stream Ecology. *Journal of the North American Benthological Society*, 7(4):433–455.

Reynolds, S. K. and Benke, A. C. (2005). Temperature-dependent growth rates of larval midges (Diptera : Chironomidae) from a southeastern US stream. *Hydrobiologia*, 544:69–75.

Rier, S. T., Tuchman, N. C., Wetzel, R. G., and Teeri, J. A. (2002). Elevated-CO2-induced changes in the chemistry of quaking aspen (Populus tremuloides Michaux) leaf litter: subsequent mass loss and microbial response in a stream ecosystem. *Journal of the North American Benthological Society*, 21(1):16–27.

Rixon, C. A. M., Duggan, I. C., Bergeron, N. M. N., Ricciardi, A., and Macisaac, H. J. (2005). Invasion risks posed by the aquarium trade and live fish markets on the Laurentian Great Lakes. *Biodiversity and Conservation*, 14(6):1365–1381.

Root, R. B. (1967). Niche Exploitation Pattern of Blue-gray Gnatcatcher. *Ecological Monographs*, 37(4):317–&.

Rosenzweig, M. L., A. Z. (1993). How are diversity and productivity related? In Ricklefs, R. E. and Schluter, D., editors, *Species diversity in ecological communities: historical and geographical perspectives.*, pages 52–65. University of Chicago Press, Chicago.

Rykiel, E. J. (1996). Testing ecological models: The meaning of validation. *Ecological Modelling*, 90(3):229–244.

Sagoff, M. (2005). Do non-native species threaten the natural environment? *Journal of Agricultural & Environmental Ethics*, 18(3):215–236.

Sagoff, M. (2007). Are nonnative species harmful? *Conservation Magazine*, 8:20–21.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., and Wall, D. H. (2000). Biodiversity - Global biodiversity scenarios for the year 2100. *Science*, 287(5459):1770–1774.

Sala, O. E., Lauenroth, W. K., McNaughton, S. J., Rusch, G., and Zhang, X. (1996). Biodiversity and ecosystem function in grasslands. In Mooney, H. A., Cushman, J. H., Medina, E., Sala, O. E., and Schulze, E. D., editors, *Functional role of biodiversity: a global perspective*, pages 129–145. Wiley,, New York.

Sandin, P. (1999). Dimensions of the precautionary principle. *Human and Ecological Risk Assessment*, 5(5):889–907.

Sandstrom, O., Abrahamsson, I., Andersson, J., and Vetemaa, M. (1997). Temperature effects on spawning and egg development in Eurasian perch. *Journal of Fish Biology*, 51(5):1015–1024.

Scheffer, M. (1990). Multiplicity of Stable States In Fresh-water Systems. *Hydrobiologia*, 200:475–486.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413(6856):591–596.

Scheffer, M., Hosper, S. H., Meijer, M. L., Moss, B., and Jeppesen, E. (1993). Alternative Equilibria In Shallow Lakes. *Trends In Ecology & Evolution*, 8(8):275–279.

Schiedek, D., Sundelin, B., Readman, J. W., and Macdonald, R. W. (2007). Interactions between climate change and contaminants. *Marine Pollution Bulletin*, 54(12):1845–1856.

Schindler, D. E. (2007). Fish extinctions and ecosystem functioning in tropical ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 104(14):5707–5708.

Schindler, D. E., Kitchell, J. F., He, X., Carpenter, S. R., Hodgson, J. R., and Cottingham, K. L. (1993). Food-web Structure and Phosphorus Cycling In Lakes. *Transactions of the American Fisheries Society*, 122(5):756–772.

Schlapfer, F. and Schmid, B. (1999). Ecosystem effects of biodiversity: A classification of hypotheses and exploration of empirical results. *Ecological Applications*, 9(3):893–912.

Schmitz, O. J. (2006). Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology*, 87(6):1432–1437.

Schreiber, A. (2009). Comparative allozyme genetics and range history of the European river barbel (Teleostei, Cyprinidae: Barbus barbus) in the Rhine/upper Danube contact area. *Journal of Zoological Systematics and Evolutionary Research*, 47(2):149–159.

Schrödinger, E. (1944). *What is Life?* Cambridge University Press.

Schwartz, M. W., Brigham, C. A., Hoeksema, J. D., Lyons, K. G., Mills, M. H., and van Mantgem, P. J. (2000). Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia*, 122(3):297–305.

Schwoerbel, J. (1999). *Einführung in die Limnologie*. Spektrum Akademischer Verlag.

Sheldon, F. and Walker, K. F. (1997). Changes in biofilms induced by flow regulation could explain extinctions of aquatic snails in the lower River Murray, Australia. *Hydrobiologia*, 347:97–108.

Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., Cooper, S. D., and Halpern, B. S. (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, 5(6):785–791.

Shurin, J. B. and Seabloom, E. W. (2005). The strength of trophic cascades across ecosystems: predictions from allometry and energetics. *Journal Of Animal Ecology*, 74(6):1029–1038.

Simberloff, D. (2007). Given the stakes, our modus operandi in dealing with invasive species should be "guilty until proven innocent.". *Conservation Magazine*, 8(2):18–19.

Sims, D. W., Wearmouth, V. J., Genner, M. J., Southward, A. J., and Hawkins, S. J. (2004). Low-temperature-driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology*, 73(2):333–341.

Sims, D. W., Wearmouth, V. J., Southall, E. J., Hill, J. M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G. C., Righton, D., Metcalfe, J., Nash, J. P., and Morritt, D. (2006). Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology*, 75(1):176–190.

Smith, P., Leah, R., and Eaton, J. (1998). A review of the current knowledge on the introduction, ecology and management of zander, Stizostedion lucioperca, in UK. In Cowx, I., editor, *Stocking and introduction of fish*, pages 209–224. Fishing News Books, Oxford, UK.

Smith, P. A., Leah, R., and Eaton, J. (1997). Removal as an option for management of an introduced piscivorous fish - the zander. In Tilzey, R. and Roberts, J., editors, *Controlling carp : exploring the options for Australia*. CSIRO Land and Water.

Smith, P. A., Leah, R. T., and Eaton, J. W. (1994). The impact of zander (Stizostedion lucioperca L.), an alien piscivore, on prey fish populations in a heavily-trafficked canal: implications for fishery management. In *The 25th Institute of Fisheries Management Annual Study Conference*, pages 133–140. The University of Lancaster.

Smith, P. A., Leah, R. T., and Eaton, J. W. (1996). Removal of pikeperch (Stizostedion lucioperca) from a British Canal as a management technique to reduce impact on prey fish populations. *Annales Zoologici Fennici*, 33(3-4):537–545.

Solan, M., Cardinale, B. J., Downing, A. L., Engelhardt, K. A. M., Ruesink, J. L., and Srivastava, D. S. (2004). Extinction and ecosystem function in the marine benthos. *Science*, 306(5699):1177–1180.

Sole, R. V., Alonso, D., and McKane, A. (2002). Self-organized instability in complex ecosystems. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 357(1421):667–681.

Sole, R. V. and Bascompte, J. (2006). *Self-organization in complex ecosystems*. Princeton University Press, Princeton.

Sole, R. V. and Montoya, J. M. (2001). Complexity and fragility in ecological networks. *Proceedings of the Royal Society B-biological Sciences*, 268(1480):2039–2045.

Sole, R. V. and Valls, J. (1992). Nonlinear Phenomena and Chaos In A Monte-carlo Simulated Microbial Ecosystem. *Bulletin of Mathematical Biology*, 54(6):939–955.

Srivastava, D. S., Cardinale, B. J., Downing, A. L., Duffy, J. E., Jouseau, C., Sankaran, M., and Wright, J. P. (2009). Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology*, 90(4):1073–1083.

Stachowicz, J. J., Graham, M., Bracken, M. E. S., and Szoboszlai, A. I. (2008). Diversity Enhances Cover and Stability of Seaweed Assemblages: the Role of Heterogeneity and Time. *Ecology*, 89(11):3008–3019.

Stachowicz, J. J., Whitlatch, R. B., and Osman, R. W. (1999). Species diversity and invasion resistance in a marine ecosystem. *Science*, 286(5444):1577–1579.

Strayer, D. L. (2009). Twenty years of zebra mussels: lessons from the mollusk that made headlines. *Frontiers In Ecology and the Environment*, 7(3):135–141.

Strong, D. R. (1992). Are Trophic Cascades All Wet - Differentiation And Donor-Control In Speciose Ecosystems. *Ecology*, 73(3):747–754.

Szargut, J., Morris, D. R., and Steward, F. R. (1988). *Exergy Analysis of Thermal, Chemical, and Metallurgical Processes*. Springer-Verlag.

Tachet, H., Bournaud, M., P., R., and Usseglio-Polatera, P. (2000). *Invertébrés d'eau douce : systématique, biologie, écologie.* CNRS Editions.

Taylor, A. A. L., Britton, J. R., and Cowx, I. G. (2004). Does the stock density of stillwater catch and release fisheries affect the growth performance of introduced cultured barbel? *Journal of Fish Biology*, 65:308–313.

Thebault, E., Huber, V., and Loreau, M. (2007). Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos*, 116(1):163–173.

Thebault, E. and Loreau, M. (2003). Food-web constraints on biodiversity-ecosystem functioning relationships. *Proceedings of the National Academy of Sciences of the United States of America*, 100(25):14949–14954.

Thebault, E. and Loreau, M. (2005). Trophic interactions and the relationship between species diversity and ecosystem stability. *American Naturalist*, 166(4):E95–E114.

Thebault, E. and Loreau, M. (2006). The relationship between biodiversity and ecosystem functioning in food webs. *Ecological Research*, 21(1):17–25.

Thomson, J. R., Lake, P. S., and Downes, B. J. (2002). The effect of hydrological disturbance on the impact of a benthic invertebrate predator. *Ecology*, 83(3):628–642.

Tilman, D. and Downing, J. A. (1994). Biodiversity and Stability In Grasslands. *Nature*, 367(6461):363–365.

Tilman, D., Lehman, C. L., and Thomson, K. T. (1997). Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the National Academy of Sciences of the United States of America*, 94(5):1857–1861.

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., and Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, 294(5543):843–845.

Townsend, C. R. (2003). Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams. *Conservation Biology*, 17:38–47.

Tuchman, N. C., Wetzel, R. G., Rier, S. T., Wahtera, K. A., and Teeri, J. A. (2002). Elevated atmospheric CO2 lowers leaf litter nutritional quality for stream ecosystem food webs. *Global Change Biology*, 8(2):163–170.

Uchida, S., Drossel, B., and Brose, U. (2007). The structure of food webs with adaptive behaviour. *Ecological Modelling*, 206(3-4):263–276.

Ulanowicz, R. E. and AbarcaArenas, L. G. (1997). An informational synthesis of ecosystem structure and function. *Ecological Modelling*, 95(1):1–10.

Ulanowicz, R. E., Jorgensen, S. E., and Fath, B. D. (2006). Exergy, information and aggradation: An ecosystems reconciliation. *Ecological Modelling*, 198(3-4):520–524.

van Dijk, P. L. M., Staaks, G., and Hardewig, I. (2002). The effect of fasting and refeeding on temperature preference, activity and growth of roach, Rutilus rutilus. *Oecologia*, 130(4):496–504.

Vander Zanden, M. J., Casselman, J. M., and Rasmussen, J. B. (1999). Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, 401(6752):464–467.

Vander Zanden, M. J. and Rasmussen, J. B. (1999). Primary consumer delta C-13 and delta N-15 and the trophic position of aquatic consumers. *Ecology*, 80(4):1395–1404.

Vandermeer, J., de la Cerda, I. G., Perfecto, I., Boucher, D., Ruiz, J., and Kaufmann, A. (2004). Multiple basins of attraction in a tropical forest: Evidence for nonequilibrium community structure. *Ecology*, 85(2):575–579.

Vandermeer, J. and Yodzis, P. (1999). Basin boundary collision as a model of discontinuous change in ecosystems. *Ecology*, 80(6):1817–1827.

Varley, M. E. (1967). *British Freshwater Fishes: Factors Affecting Their Distribution*. Blackwell Scientific Publications, Oxford.

Vilizzi, L., Copp, G. H., Carter, M. G., and Penaz, M. (2006). Movement and abundance of barbel, Barbus barbus, in a mesotrophic chalk stream in England. *Folia Zoologica*, 55(2):183–197.

Vitousek, P. M., Loope, L. L., and Stone, C. P. (1987). Introduced Species In Hawaii - Biological Effects and Opportunities For Ecological Research. *Trends In Ecology & Evolution*, 2(7):224–227.

Vitule, J. R. S., Freire, C. A., and Simberloff, D. (2009). Introduction of non-native freshwater fish can certainly be bad. *Fish and Fisheries*, 10(1):98–108.

Voinov, A. (2002). Teaching and learning ecological modeling over the web: a collaborative approach. *Conservation Ecology*, 6(1).

Volterra, V. (1926). *Animal ecology*. McGraw-Hill, New York.

Walker, B., Kinzig, A., and Langridge, J. (1999). Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. *Ecosystems*, 2(2):95–113.

Walker, B. H. (1992). Biodiversity and Ecological Redundancy. *Conservation Biology*, 6(1):18–23.

Walker, B. H., Langridge, J. L., and McFarlane, F. (1997). Resilience of an Australian savanna grassland to selective and non-selective perturbations. *Australian Journal of Ecology*, 22(2):125–135.

Wall, G. (1986). *Exergy- A Useful Concept*. PhD thesis, Physical Resource Theory Group, Chalmers University of Technology, Goteborg, Sweden.

Webb, B. W. (1996). Trends in stream and river temperature. *Hydrological Processes*, 10(2):205–226.

Welcomme, R. (1988). International introductions of inland aquatic species. Tech. Pap. 294, FAO.

Werner, E. E. and Gilliam, J. F. (1984). The Ontogenetic Niche and Species Interactions in Size-Structured Populations. *Annual Review of Ecology and Systematics*, 15:393–425.

Westlake, D. F., Casey, H., Dawson, H., Ladle, M., Mann, R. H. K., and Marker, A. F. H. (1972). The chalk stream ecosystem. In Kajak, Z. and Hillbricht-Ilkowska, A., editors, *Productivity Problems of Freshwaters*, pages 615–635, Warsaw, Poland. Proceedings of the International Biological Programme-Unesco Symposium, Illus. Maps. Polish Scientific Publishers.

Wheeler, A. and Jordan, D. R. (1990). The Status of the Barbel, Barbus-barbus (l) (teleostei, Cyprinidae), In the United-kingdom. *Journal of Fish Biology*, 37(3):393–399.

Wheeler, A. and Maitland, P. S. (1973). Scarcer Freshwater Fishes of British-isles .1. Introduced Species. *Journal of Fish Biology*, 5(1):49–68.

White, P. C. L., Ford, A. E. S., Clout, M. N., Engeman, R. M., Roy, S., and Saunders, G. (2008). Alien invasive vertebrates in ecosystems: pattern, process and the social dimension. *Wildlife Research*, 35(3):171–179.

Wikramanayake, E. and Moyle, P. (1989). Ecological structure of tropical fish assemblages in wet-zone streams of Sri Lanka. *Journal of Zoology*, 218:503–526.

Wilbur, H. M. (1997). Experimental ecology of food webs: Complex systems in temporary ponds - The Robert H. MacArthur Award Lecture - Presented 31 July 1995 Snowbird, Utah. *Ecology*, 78(8):2279–2302.

Williams, R. J. and Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774):180–183.

Willis, A. J. (1997). The ecosystem: An evolving concept viewed historically. *Functional Ecology*, 11(2):268–271.

Wilson, M. A. and Carpenter, S. R. (1999). Economic valuation of freshwater ecosystem services in the United States: 1971-1997. *Ecological Applications*, 9(3):772–783.

Winemiller, K. O. and Jepsen, D. B. (1998). Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology*, 53:267–296.

Winkelmann, C., Hellmann, C., Worischka, S., Petzoldt, T., and Benndorf, J. (2011). Fish predation affects the structure of a benthic community. *Freshwater Biology*.

Witkowski, A. (2006). NOBANIS - Invasive Alien Species Fact Sheet - Pseudorasbora parva. *Online Database of the North European and Baltic Network on Invasive Alien Species*.

Wojdak, J. M. (2005). Relative strength of top-down, bottom-up, and consumer species richness effects on pond ecosystems. *Ecological Monographs*, 75(4):489–504.

Wood, P. J. and Petts, G. E. (1999). The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes*, 13(3):387–399.

Woodiwiss, F. S. (1964). The Biological System of Stream Classification Used By the Trent-river-board. *Chemistry & Industry*, (11):443–447.

Woodward, G. (2009). Biodiversity, ecosystem functioning and food webs in fresh waters: assembling the jigsaw puzzle. *Freshwater Biology*, 54(10):2171–2187.

Woodward, G., Ebenman, B., Ernmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., and Warren, P. H. (2005a). Body size in ecological networks. *Trends in Ecology & Evolution*, 20(7):402–409.

Woodward, G. and Hildrew, A. G. (2001). Invasion of a stream food web by a new top predator. *Journal of Animal Ecology*, 70:273–288.

Woodward, G. and Hildrew, A. G. (2002). Body-size determinants of niche overlap and intraguild predation within a complex food web. *J. Anim. Ecol.*, 71(6):1063–1074.

Woodward, G., Papantoniou, G., Edwards, F., and Lauridsen, R. B. (2008). Trophic trickles and cascades in a complex food web: impacts of a keystone predator on stream community structure and ecosystem processes. *OIKOS*, 117(5):683–692.

Woodward, G., Perkins, D. M., and Brown, L. E. (2010). Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B-biological Sciences*, 365(1549):2093–2106.

Woodward, G., Speirs, D. C., and Hildrew, A. G. (2005b). Quantification and resolution of a complex, size-structured food web. In *Advances in Ecological Research*, pages 85–135.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H. K., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Stachowicz, J. J., and Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314(5800):787–790.

Worsfold, N. T., Warren, P. H., and Petchey, O. L. (2009). Context-dependent effects of predator removal from experimental microcosm communities. *Oikos*, 118(9):1319–1326.

Wright, J. F., Clarke, R. T., Gunn, R. J. M., Kneebone, N. T., and Davy-Bowker, J. (2004). Impact of major changes in flow regime on the macroinvertebrate assemblages of four chalk stream sites, 1997-2001. *River Research and Applications*, 20(7):775–794.

Wright, J. F., Gunn, R. J. M., Winder, J. M., Blackburn, J. H., and Wiggers, R. (2001). The response of chalk stream macroinvertebrates to a prolonged drought: The value of a long-term dataset. *International Association of Theoretical and Applied Limnology, Vol 27, Pt 2, Proceedings*, 27:912–915.

Wright, J. F., Moss, D., Armitage, P. D., and Furse, M. T. (1984). A Preliminary Classification of Running-water Sites In Great-britain Based On Macroinvertebrate Species and the Prediction of Community Type Using Environmental Data. *Freshwater Biology*, 14(3):221–256.

Wright, J. F. and Symes, K. L. (1999). A nine-year study of the macroinvertebrate fauna of a chalk stream. *Hydrological Processes*, 13(3):371–385.

Xenopoulos, M. A., Lodge, D. M., Alcamo, J., Marker, M., Schulze, K., and Van Vuuren, D. P. (2005). Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Global Change Biology*, 11(10):1557–1564.

Xu, C. L., Letcher, B. H., and Nislow, K. H. (2010). Context-specific influence of water temperature on brook trout growth rates in the field. *Freshwater Biology*, 55(11):2253–2264.

Yodzis, P. (1988). The Indeterminacy of Ecological Interactions As Perceived Through Perturbation Experiments. *Ecology*, 69(2):508–515.

Yvon-Durocher, G., Montoya, J. M., Emmerson, M. C., and Woodward, G. (2008). Macroecological patterns and niche structure in a new marine food web. *Central European Journal of Biology*, 3(1):91–103.

Zavaleta, E. S. and Hulvey, K. B. (2004). Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science*, 306(5699):1175–1177.

Zieba, G., Copp, G. H., Davies, G. D., Stebbing, P., Wesley, K. J., and Britton, J. R. (2010). Recent releases and dispersal of non-native fishes in England and Wales, with emphasis on sunbleak Leucaspius delineatus. *Aquatic Invasions*, 5(2):155–161.